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EXPERIMENTAL MORPHOGENESIS IN ADVENTITIOUS BUDS OF FLAX

By Heather F. Gulline*

[*Manuscript received June 12, 1959*]

Summary

The polar development of adventitious buds and their associated vascular traces in flax hypocotyls has been studied, and experiments performed with the object of altering this polarity.

Buds were induced on portions of epidermal tissue grafted in inverted positions on hypocotyls, and on hypocotyls subjected to reversal of the direction of gravity and electric polarity normally acting on them.

The effects of experimental incisions into adventitious meristems, and in close proximity to them, were also studied.

The basic pattern of development remained constant under all treatments.

These experiments show that the epidermal and cortical cells from which the adventitious buds and their dependent vascular traces develop possess a very strong inherent polarity which could not be varied by extracellular changes of field.

I. Introduction

It is well known that if young seedlings of flax (*Linum usitatissimum* L.) are decapitated below the cotyledons they will give rise to numerous adventitious buds on the epidermis of the remaining hypocotyl.

Each bud originates from a meristem developed by the dedifferentiation of mature epidermal cells, and is independent of its neighbours. The mode of initiation and course of development of the buds have been described in detail by Crooks (1933) and Link and Eggers (1946). It has been shown that light, auxin concentration, and nutritional level affect the number of buds produced (Link and Eggers 1938; Eggers 1946). However, the conditions determining which particular epidermal cells dedifferentiate and give rise to meristems are not known. An examination of the material when a meristem is first identifiable shows no underlying structural specialization which might be responsible for its initiation. It is only at a much later stage, when several leaf primordia are identifiable, that vascular bundles become differentiated in the cortex between the bud and the stele of the hypocotyl.

In spite of the absence of any recognizable organizing structures, an adventitious bud and its related vascular traces follow a predictable pattern of development. The normal epidermal bud is asymmetric in form even at the "bulge" stage (term used by Link and Eggers (1946)), although developed from uniform and apparently non-polar tissue, and has a well-defined polarity in relation to the plant as a whole.

It is possible to study the effect of experimental incisions and other stimuli on the morphogenesis of these buds without the complication of the subjacent vascular traces normally associated with apical meristems. In addition, the absence of enclosing leaves gives access to the apex without damage to neighbouring tissues.

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The results of experimental treatments are readily visible. The epidermal buds of flax therefore appear to offer an excellent material for investigating the factors influencing morphogenesis.

In the experiments described here, the normal development of buds has been modified by incisions into either their meristems or the subjacent cortical tissue through which vascular connections would normally be formed. Experiments have also been performed with the object of reversing bud polarity by the application of external stimuli to the hypocotyls and by inverted grafting techniques, both prior to the initiation of buds and during the course of their growth. Although the experimental treatments did not result in any variation in the polarity of adventitious buds, the manner of expression of the inherent polarity of epidermal and cortical cells in new tissues derived from them by dedifferentiation is of interest.

For these experiments it was important to be able to induce bud development in a selected region of a hypocotyl, and to stimulate continued growth of experimentally treated buds. It was also necessary to suppress the development of too many additional buds on experimental plants. Techniques developed to meet these needs are described.

This work is part of a general study in this Laboratory of the manner in which plant development is regulated.

II. Materials and Methods

(*a*) *Preparation of Material*

Flax seeds of the variety "Ventnor" were soaked for 2 min in absolute alcohol, rinsed well with water, and planted in dishes of washed quartz gravel moistened with dilute Knop's solution (0·6 g total salts/litre). The dishes of seedlings were kept in a well-lit greenhouse at a temperature of approximately 20°C. At the age of 1 week, when the cotyledons were fully expanded, the seedlings were decapitated 1–2 mm below the cotyledons. Adventitious buds usually began to appear in the upper regions of such decapitated seedlings after a further 5 or 6 days, and rapidly increased in size and number for the following few days. After about 2 weeks, one or more buds on each hypocotyl usually outgrew the others. As no artificial light was supplied, the above times were subject to modification by weather conditions. Buds grown under these conditions were used for the study of "normal" growth.

For use in laboratory experiments, seedlings were removed from the gravel at the time of decapitation, their roots wrapped in cotton wool wet with tap water, and placed in petri dishes on moist filter paper, or in individual 2 by $\frac{1}{2}$ in. specimen tubes kept upright in a closed transparent plastic dish. Buds were induced on these seedlings by placing their containers under a daylight fluorescent lamp so that they received constant illumination at an intensity of about 1000 lumens/sq. ft. Initiating meristems then became visible as bulges about 100 μ long after 3 or 4 days. The number of buds per seedling was kept as low as possible by removing the plants from continuous light after the first bulges appeared and giving them only 4 hours' illumination per day. This was sufficient to promote further growth in existing meristems, but induced few if any new ones. Only one bud per plant was used for incision experiments, surplus buds being removed to avoid any possibility of competitive or mutually inhibitory effects between buds.

For some experiments it was desired to induce bud initiation on particular regions of epidermis, e.g. on previously incised or grafted portions. This was done by surrounding the hypocotyl with a suitable length of opaque black plastic tubing of 2 mm bore, with a small "window" cut out to expose the desired bud initiation area. The plants were then placed under continuous strong light until buds appeared on the exposed epidermis. The occasional buds which developed on the shaded portions were excised.

Buds treated in the incision experiments to be described were stimulated to continue growing by redecapitating the hypocotyl just above their upper limit.

For histological examination, hypocotyls bearing treated buds, or controls, were fixed in Carnoy's solution, paraffin-embedded and sectioned, stained in safranin and haematoxylin, and mounted in balsam. Young buds were also studied by stripping the epidermis bearing them from the hypocotyl with forceps. These were stained in haematoxylin and mounted flat.

Whole mounts were made by fixing hypocotyls as above, placing them in lactic acid (B.P.) in an oven at about 60°C for 4 hr, or longer if necessary, to clear, and mounting between large cover slips in glycerine jelly. When viewed by dark field illumination, meristematic areas, vascular tissues, and callus formations were clearly visible.

Incision and grafting experiments were carried out in a glass-topped box inside which an atomizing spray maintained a saturated atmosphere. A high power dissecting microscope and two spotlights were mounted above the box. Microscalpels were made from portions of thin razor blades screwed on to brass holders.

Inverted grafts of epidermal tissue were made by excising the selected portion of tissue with a finely pointed razor blade knife, rotating it through 180°, and replacing it in close contact with the exposed cortex from which it was originally taken. The liberated contents of damaged cells acted as an adhesive and no other means of holding the grafts in place was used. The ends of such grafted strips usually curled up a little, probably due to shrinkage of damaged cells, but in most cases the central portion retained sufficient points of contact to permit a graft union to develop.

(*b*) *Normal Development of Adventitious Buds*

A detailed study of the initiation and growth of adventitious buds in the variety "Ventnor" of flax used in these experiments showed that their course of development did not differ from that described by previous authors. However, in our material there was no evidence of the formation of adventitious buds by intact seedlings, as described by Link and Eggers (1946). Nor were dormant meristemoids ever observed in the epidermis of the flax used for these experiments. The effects of treatments used prior to or immediately after decapitation would therefore have been observable in adventitious buds which developed subsequently.

It is not necessary to repeat here a full account of morphogenesis in the adventitious buds, but some new observations are reported. Previous authors have not described the well-marked polarity usually observable in young adventitious meristems. In a large number of early meristems observed on stripped portions of epidermis, and in tangential and longitudinal sections, there was a marked inequality in both cell size and density of cytoplasmic contents between the upper and lower halves. This was clearly noticeable at the bulge stage (Plate 1, Fig. 1), and was sometimes recognizable when only one or two epidermal cells had dedifferentiated. This inequality within the bulge appears to be correlated with the position of the first leaf primordium. When the first leaf primordium arises, in 85 per cent. of cases it forms from the basal quadrant of the meristematic area. The other 15 per cent. of buds develop their first leaves in various positions from the flanks to the upper end of the meristematic area.

The inequality between cells of the upper and lower halves becomes more marked as growth proceeds. As a result, the developing bud axis is inclined at an angle of approximately 60° from the vertical axis of the hypocotyl. An allied effect is the buttressing of the base of the developing shoot. This is clearly identifiable by the time the first one or two leaf primordia are visible (see Crooks's (1933) illustrations), even when the first leaf primordium develops from the upper side of the bulge. Thus the future orientation of a developing shoot can be recognized before its axis or vascular tissues have developed. It is possible to identify by macroscopic inspection the orientation of buds produced under experimental treatments. This method was used in association with microscopic examination.

The development of vascular traces in association with adventitious buds in flax has been described by Crooks (1933). It should be emphasized that the preliminary divisions of cortical cells extend along a strictly basipetal and centripetal route. The procambium so formed gives rise to vascular traces which may at first appear to be discontinuous, as the lignification of xylem elements is sometimes not consecutive. Finally, when the vascular trace is completely differentiated, considerable extension growth appears to take place, as in developing shoots. In older material, this results in a contorted appearance of the vascular trace within the cortex. If serial sections of such twisted vascular bundles are traced, it is found that the overall route is always basipetal from bud to stele.

III. Experimental Procedures and Results

The following experiments were performed with a view to modifying the normal course of development of adventitious buds and their associated vascular traces.

(*a*) *Inverted Grafts of Epidermal Tissue*

In the upper regions of freshly decapitated hypocotyls, portions of epidermis about 2 mm long or less, with as little cortical tissue as possible, were excised, rotated through 180°, and grafted back to their original site in an inverted position. Controls were similarly excised and grafted back with their normal orientation. Buds were induced on these scions by selective illumination.

These cortical grafts "took" readily when there was good approximation of the cut surfaces. Scar tissue was mostly absorbed after a few days, giving almost complete cellular continuity between stock and scion (see Plate 1, Figs. 2–4). Where there were air gaps because of poor fitting of the surfaces, callus cells were frequently developed from both sides, filling the space and grafting to each other.

The continued healthy growth of grafts indicated that physiological continuity was soon established, whether scions were normally orientated or inverted. This conclusion is supported by the observation of large accumulations of starch grains in a few grafts which survived in spite of very poor contact. In these exceptional cases it appeared that although the moist conditions prevailing prevented desiccation and enabled unhealed grafts to survive, there was little transport of metabolic substances between stock and scion. Thus most of the sugar produced in the scion by photosynthesis was unable to move from the scion, and was stored there as starch.

The absence of stored starch from healthy grafts with good contact suggests that it is possible for sugars and other metabolic substances to be transported through the cortex by diffusion, prior to the formation of vascular tissues.

In older decapitated hypocotyls, portions of epidermis bearing young bud primordia were similarly excised and grafted back in an inverted position.

In all cases, whether bud meristems were present at the time of grafting or not, the resulting buds retained the polarity of the cells from which they developed. Thus, on inverted grafts, buds appeared directed downward on the plant (Plate 1, Figs. 2, 3). The bud on the scion in Plate 1, Figure 3, was induced after grafting.

Vascular traces initiated by the epidermal buds developed in the original basipetal direction of the cortical cells from which they were derived. At the junction of an inverted graft with its stock, the direction of the path of dedifferentiation and subsequent development of vascular elements was immediately reversed and continued in the basipetal direction of the stock. In grafts in which callus cells intervened between the grafted tissues there was sometimes a little disorientation of tracheid-like elements within the callus growth, but strictly basipetal development of vascular bundles was maintained within the original tissues. Plate 1, Figure 4, illustrates the reversal area of a vascular trace between an inverted graft and its stock. Portions of a similar trace are also shown in Plate 1, Figure 3.

The vascular bundles made contact with the stele in the normal way described by Crooks (1933). Two strands are visible at the endodermis in Plate 1, Figure 3.

The phyllotaxis of buds on inverted grafts was normal, but the first one or two leaf primordia were of restricted development if already determined at the time of grafting.

(b) *Undercut Buds*

Diagonal incisions were made into the cortex of hypocotyls bearing adventitious buds at the bulge to early bud stages, in such a way as to sever the course normally followed by the vascular traces between the buds and the stele of the seedlings. Each bud was thus isolated from the hypocotyl except by a flap of cortical tissue at its upper side (Plate 2, Fig. 1). As controls, other hypocotyls were similarly incised immediately after decapitation. On some of these, buds were induced by the selective illumination technique.

The continued growth of such undercut meristems gave rise to buds of normal phyllotaxis. Any leaf primordia which were already determined at the time of cutting developed only into parenchymatous structures. Leaf primordia determined after cutting developed normally.

The vascular traces of the growing buds also developed along the normal basipetal path through the cortex, ending blindly at the cut surface or in a whorl of tracheids (Plate 2, Fig. 1). Although water and nutrient substances could reach the bud only by downward diffusion through the flap of cortical tissue, there was never any indication of an acropetal development of vascular tissues from the bud along the path of the diffusion flow.

Undercut buds did not develop into long shoots under the conditions of the experiment. It appears that the diffusion of metabolic substances across the cortex was insufficient to sustain prolonged growth.

There was never any development of vascular tissue in the cortex on the adaxial side of the cut in the position where it would have formed had no incision been made. It can be inferred that each vascular trace arises in response to its bud, and is not determined by the same stimulus which determines the position of the bud.

(c) *Meristems Bisected at the Bulge Stage*

Adventitious meristems at the bulge stage were bisected by an incision penetrating into the cortex but not reaching the stele of the hypocotyl.

One bud was formed on each side of the cut from the undamaged portions of the meristem. Each bud developed independently of the other. Plate 2, Figure 2, illustrates a typical example.

The first two leaf primordia were formed in their normal positions, one at each end of the original bulge, each now being the first leaf primordium of one of the new buds. The subsequent two leaf primordia in each bud were formed from the lateral flanks of the original bulge, following which the normal 2/5 pattern of phyllotaxis was established.

A separate vascular trace developed in association with each bud, eventually connecting it to the stele of the hypocotyl in the normal way.

(d) *Wounding and Incision Experiments at Early Bud Stage*

In typical young adventitious buds in which the first leaf primordium was just distinguishable as a small mound, an incision was made separating the leaf primordium from the apical area. In one series of experiments, one or other of these isolated areas was completely excised. The behaviour of the residual portion was the same, whichever treatment was applied.

Following the isolation of the apical area from the first leaf primordium, independent buds developed on either side of the cut (Plate 2, Fig. 3). The apical area continued to grow into a normal bud with its first leaf primordium on the side distant from the cut, i.e. in the position normally occupied by the second leaf primordium. A vascular connection was formed with the stele in the usual way.

The original first leaf primordium usually continued to enlarge for a few days, then ceased growing. Histological examination showed that after the meristem was wounded, further growth of the existing first leaf primordium was due almost entirely to the enlargement of cells already present, resulting in a chiefly parenchymatous structure (Plate 2, Figs. 3, 4). A new bud frequently developed in an axillary position at its base. The first leaf primordium of the new bud usually arose on the side distant from the first leaf of the original bud, now the subtending leaf of the "axillary" bud. Further growth of the new bud followed the usual pattern of adventitious flax buds, giving the appearance of a normal adventitious bud with restricted development of the first leaf (Plate 2, Fig. 4).

(e) *Reversals of Physical Field*

The effect of the direction of the physical fields of light, gravity, and electricity on the polarity of adventitious buds and their associated vascular traces was investigated.

When decapitated hypocotyls were grown in an inverted position, with light supplied from the direction of either their bases or their upper ends, no variation was observed in the polarity of adventitious buds produced on them.

Young flax seedlings were grown in a centrifuge in such a way that they experienced a force of 40 times that of normal gravity in the direction opposite to normal, for a week. The seedlings appeared completely healthy and grew at a normal rate. When decapitated, the hypocotyls produced buds of normal polarity although centrifugation was continuous during their initiation and growth. Normal basipetal differentiation of their associated vascular traces was observed. Higher accelerations were also used for short periods but no effect was observed in buds developed on hypocotyls which experienced $900g$ for periods of 4 hr.

Small electric currents were passed continuously through decapitated hypocotyls in a direction which reversed their observed normal electrical polarity (Newman, unpublished work). Control plants were subjected to a similar current in the normal direction. Buds were induced on the hypocotyls while the current was flowing. All such buds and their vascular traces were of normal polarity.

It was concluded that the polarity exhibited by flax adventitious buds and the development of their associated vascular traces is not influenced by light, gravity, or electrical polarity.

(f) *Chemical Treatment*

In an attempt to destroy the polarity of initiating meristems, decapitated hypocotyls were treated with solutions of chloral hydrate in concentrations ranging from 1 per cent. to 0·03 per cent. while buds were being initiated.

At sublethal concentrations, chloral hydrate had no apparent effect on the polarized growth of entire flax hypocotyls, possibly not penetrating to the site of bud initiation. In previous work with chloral hydrate (Bünning 1956), treated tissues were in more intimate contact with the chemical.

IV. Discussion

The modifications of normal development in tissues resulting from these experiments are of considerable interest. On the one hand, the well-known power of dedifferentiation of mature tissues in response to various treatments is evidence of a great plasticity of function in cells of the epidermis and cortex. On the other hand, the conformation of the new structures resulting from such dedifferentiation to clearly definable "rules" of pattern and orientation, illustrates an even greater rigidity of control at the intracellular level.

It has been shown in the present work that the adventitious buds produced on the epidermis of flax hypocotyls are invariably orientated in the morphologically upward direction of the tissue from which they develop. This polarity has been traced to the asymmetrical division of the cells from which they initiate.

Incision experiments have shown that the bud vascular traces are completely dependent on their buds for their inception. It therefore appears that growth substances, presumably auxins, produced by the bud stimulate cortical cells to dedifferentiate along a route from the bud to the central stele of the hypocotyl. This route is invariably basipetal, which would indicate that the movement of the controlling growth substances is polarized. Camus (1949) has described the basipetal development of vascular tissue beneath grafted buds, and shown that a comparable effect can be produced by indolylacetic acid solution.

In the inverted epidermal graft experiments, the reversal of direction of the bud vascular trace upon crossing the line of union of the grafted tissues (see Plate 1, Fig. 4) is taken to be further evidence of the strictly polarized transport of the auxins. In *Coleus*, Jacobs (1952, 1954) has observed a small percentage of acropetal regeneration in severed xylem strands, which indicates an acropetal movement of physiological concentrations of auxin. No comparable evidence has been observed in flax. The failure of all types of experiments designed to induce an acropetal progress of cortical dedifferentiation and later differentiation of vascular tissues further supports the conclusion that the transport of growth substances from the bud is strictly basipetal.

Bünning (1956) has postulated that each cell of a plant body has an inherent polarity. The present experiments in which individual epidermal cells divide and eventually give rise to a complex and highly polarized structure in spite of all attempts to reverse this polarity may be regarded as supporting Bünning's hypothesis.

The development of two bud primordia following the bisection of a flax adventitious meristem is similar to the production of several apices when the apical meristem of a *Lupinus* shoot is subdivided (Ball 1954). In flax, as in *Lupinus*, the new apices are independent of one another and each proceeds to grow into a shoot. The independence of the two buds in flax can also be seen from the separate development of the vascular traces from each bud.

As soon as the first leaf primordium has enlarged sufficiently to be distinguishable from the rest of the meristem, a transverse incision does not produce two equal buds, but one bud develops from the true apical area, and a second one only develops much later as an axillary to the isolated leaf primordium, which is usually restricted to a parenchymatous outgrowth.

No criterion of the absolute time of leaf determination such as has been observed in *Dryopteris aristata* by Cutter (1956) has been identified. A variety of intermediate stages between a normal bud and a completely axillary bud with modified subtending leaf has been observed in buds resulting from incised meristems. These axillary buds are probably the result of incisions made when the leaf primordium was not yet visible, but was already physiologically differentiated. At no stage was it found possible to transform a visible leaf primordium into a bud. Cutter (1958) has made a similar observation, working with another angiosperm, *Nuphar*.

The experiments described here show that once initiated, adventitious meristems in flax hypocotyls behave just as shoot apical meristems, in that they are self-regulating and cannot be permanently deranged by incisions or externally applied changes of physical field. Their early stages have imposed upon them the polarity of the mature tissues from which they are derived. No treatments yet used have succeeded in overcoming or even temporarily varying this polarity, which is expressed in the unfailing acropetal orientation of adventitious buds, and basipetal differentiation of their associated vascular tissues. The source of this polarity appears to be intracellular and inherent in each cell of the plant body.

V. Acknowledgments

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Explanation of Plates 1 and 2

Plate 1

Fig. 1.—Longitudinal section through an adventitious meristem at the "bulge" stage. Note inequality between cells of upper and lower halves. ×320.

Fig. 2.—Longitudinal section of an inverted graft of a small bud, at "early bud" stage. No vascular tissues have developed. A good graft union has formed via callus cells. ×110. *a*, *b*, Extremities of grafted portion. Arrows indicate morphologically downward direction of tissues.

Fig. 3.—Longitudinal section of an inverted epidermal graft on which a bud has been induced. A vascular connection has been formed from the bud to the stele of the hypocotyl, in the morphogenetically downward direction in each tissue (indicated by arrows). ×110.

Fig. 4.—Longitudinal section of the reversal area of the vascular trace developed between an inverted bud graft and the stele of the hypocotyl. ×270. *sc*, Scion. *st*, Stock. Arrows indicate morphologically downward direction of tissues.

Plate 2

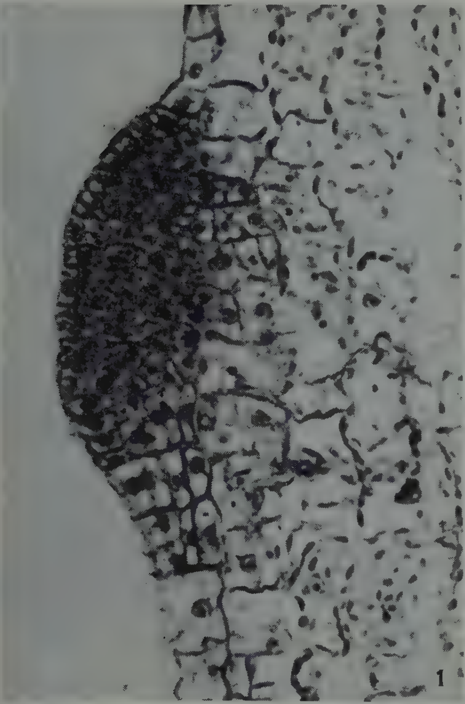
Fig. 1.—Longitudinal section of an undercut bud which has developed an extensive "nest" of tracheids in a whorled callus at the basal tip of the flap. No vascular tissues have developed through the upper portion of the flap. ×53.

Fig. 2.—Longitudinal section of a transversely bisected meristem which has given rise to two bud primordia, each with its own prevascular trace. ×135.

Fig. 3.—Longitudinal section of a transversely cut "early bud", which had one leaf primordium visible when cut. *b*.1, bud developed from original apical area. *b*.2, bud developed in axil of original leaf primordium. *l.p*.1, original leaf primordium. ×135.

Fig. 4.—Longitudinal section through a bud whose original apical area was excised when the first leaf primordium was visible. The first leaf primordium (*l.p*.1) has become a simple parenchymatous structure, and a new bud has developed in its axil. ×90.

EXPERIMENTAL MORPHOGENESIS IN FLAX BUDS



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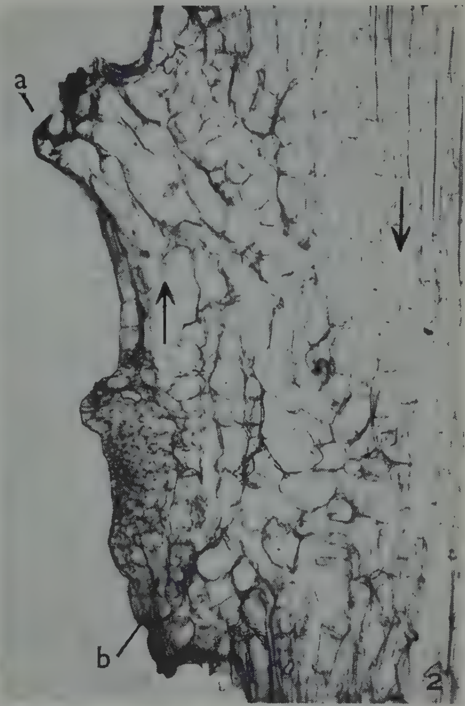

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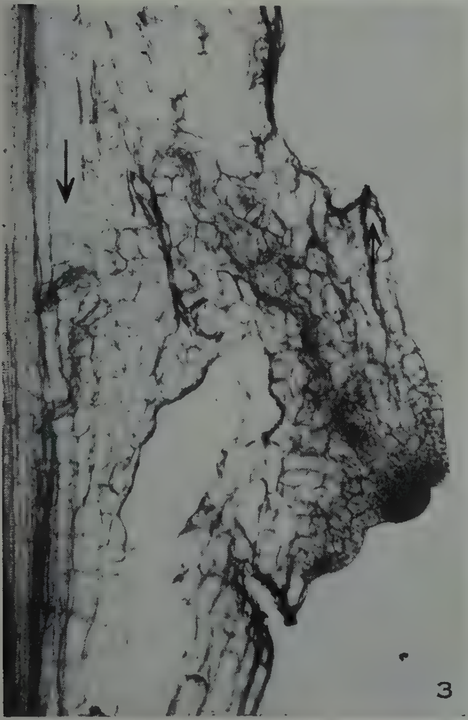

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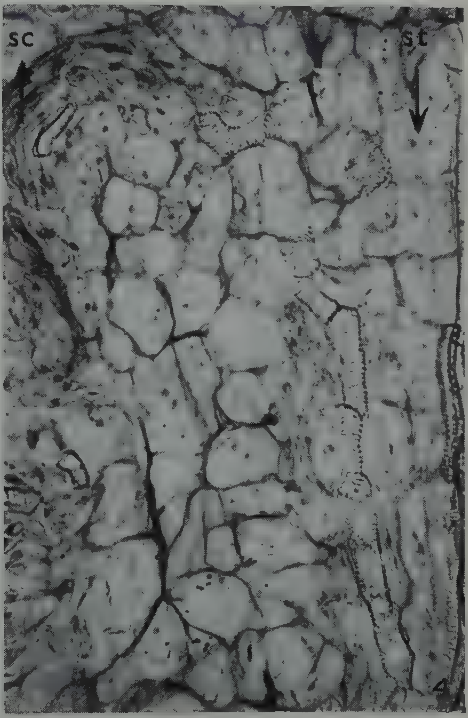

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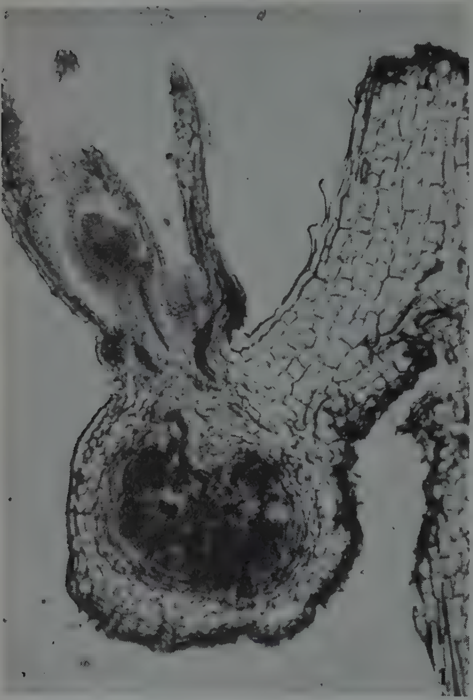
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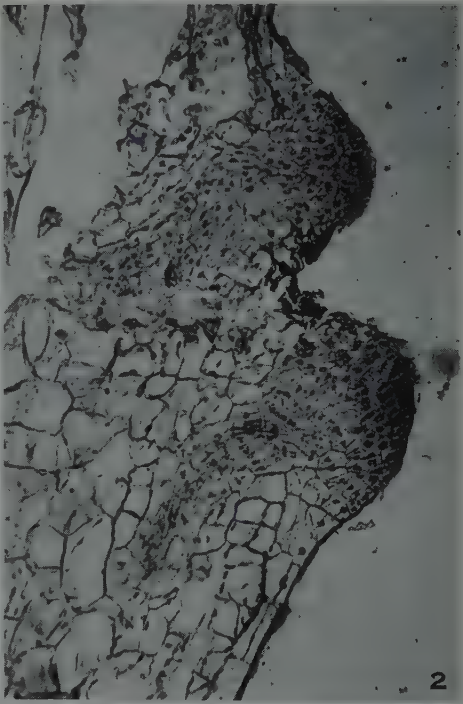
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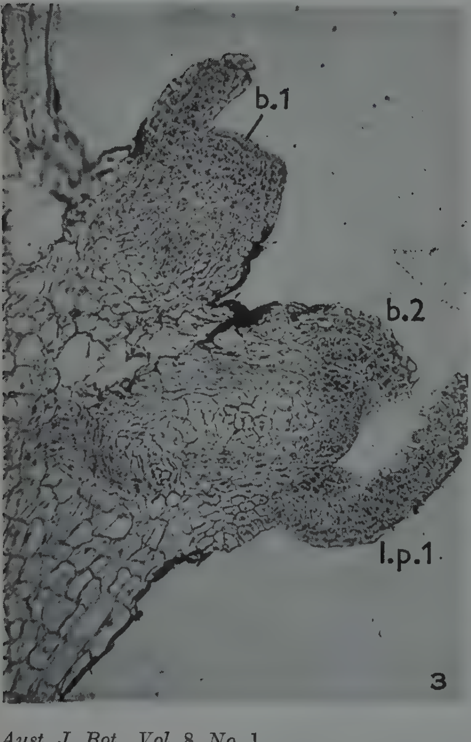
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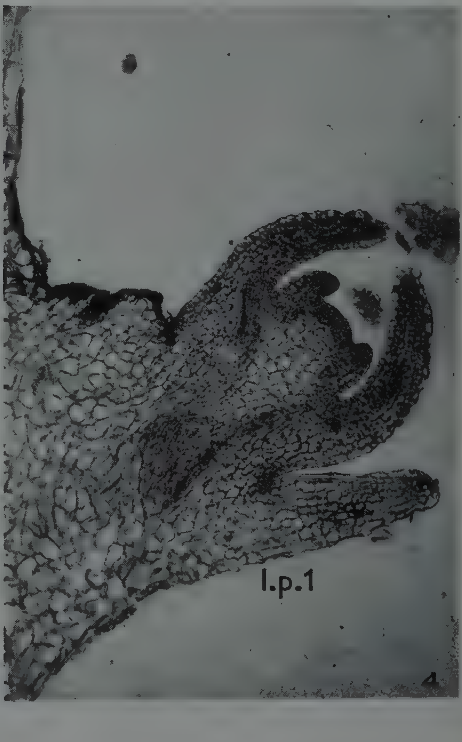
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OBSERVATIONS ON THE GAMETOPHYTES OF *GRAMMITIS BILLARDIERI* WILLD. AND *CTENOPTERIS HETEROPHYLLA* (LABILL.) TINDALE (GRAMMITIDACEAE)

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Summary

An account is given of the spores, germination, and vegetative features of the prothalli of *Grammitis billardieri* and *Ctenopteris heterophylla*, and of the reproductive organs of *G. billardieri*.

The characteristic germination is unlike that found in other ferns. The trilete green spore frequently divides in the unruptured sporangium and the first division produces two equal prothallial cells. Growth is extremely slow, the filament long and often branched, and the rhizoids which appear late may branch. The first longitudinal division occurs in a cell back from the apex, and the gametophyte at maturity is elongated and ribbon-like, with or without a slightly indented apex, brown marginal rhizoids, and discontinuous axial cushions two to three cells thick. The thallus, which is extremely slow in reaching maturity, is dark green, and the walls perpendicular to the surface are pitted. Regeneration is common.

The most distinctive feature of the gametophyte of *G. billardieri* is the development of characteristic spine-like hairs unlike those found on fern prothalli of other families. These hairs are marginal in the anterior region and develop from wedge-shaped initial cells. They differ in form and origin from those found in members of the Polypodiaceae.

The antheridia appear at an unusual stage in development, occurring after some of the archegonia have been produced and forming with them on the cushions. The archegonia have longer necks and the antheridia are slightly more complex than those found in members of the Polypodiaceae which have been investigated.

It is considered that the separation of the family Grammitidaceae from the Polypodiaceae on sporophytic characters is supported by the gametophytic generation of the two Victorian grammitid ferns *G. billardieri* and *C. heterophylla*.

I. INTRODUCTION

Grammitis billardieri Willd. and *Ctenopteris heterophylla* (Labill.) Tindale, the two Victorian members of the *Grammitis* group of ferns, were formerly included in the genus *Polypodium* in the family Polypodiaceae. Ching (1940, paper not seen), Holttum (1947, 1949), Copeland (1952), and Alston (1956) raised the *Grammitis* group to family status. The change was based on the fact that this group differed from the true Polypodiaceae in the anatomical structure of their rhizomes and stipes, their distinctive hairs, and green trilete spores (Holttum 1954). Copeland makes no suggestion as to the phyletic origin of the Grammitidaceae, but Holttum considered that they were possibly derived from the Gleicheniaceae. Ching does not separate *Ctenopteris* Blume from *Grammitis* Swartz, while Copeland and Holttum, though emphasizing the close relationship between the two, recognize *Ctenopteris* and *Grammitis* as separate genera.

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Grammitis billardieri has had 14 synonyms (Copeland 1951), *Polypodium billardieri* R.Br. being the one previously used in Victoria. *Ctenopteris heterophylla* was formerly *Polypodium grammitidis* R.Br., synonym *Grammitis heterophylla* Labill.

There are few references in the literature to the gametophytic generation of the *Grammitis* group, and the only description is one given by Goebel (1888) for the mature prothallus of the tropical fern *Polypodium obliquatum* Bl. (now *Ctenopteris obliquata* (Bl.) Holtt. comb. nov. (Holttum 1954)), found in the vicinity of Tjibodas (Java). This fern was also called *Grammitis obliquatum* Hassk. (Stokey 1951). A figure of this prothallus and its hairs is given by Goebel (1905). Copeland and Giauque (1950) make a brief reference without figures to the distinctive gametophytes of the Grammitidaceae grown by Giauque.

II. Material and Methods

Grammitis billardieri is a variable species and has a wide range from Antarctic America to New Zealand, Tasmania, and the eastern states of Australia. The Victorian plant is a small epiphyte growing chiefly on mossy logs and the lower parts of tree fern trunks in wet forest gullies, where light intensity is low and humidity high. The plants, however, are able to withstand dry conditions for some time. The leaves are thick and the mesophyll tissue is very loosely arranged, with large intercellular spaces. The sporangium has an annulus composed of an average of 12 cells, the range being 11 to 16. Copeland (1951) considered *G. billardieri* to have an average of 13 to 14, though Christensen gave 11 as the number.

Ctenopteris heterophylla is more restricted in its distribution and occurs in Victoria, Tasmania, and New Zealand. It is also an epiphyte, but grows in more exposed situations higher up the gullies and on higher branches where there is more light than is favoured by *G. billardieri*. The material was found on the mossy trunks and branches of *Olearia argophylla* F.Muell., often in the company of *Hymenophyllum cupressiforme* Labill. The fronds are thick and herbaceous, with large intercellular spaces in the mesophyll, and have a greater ability to recover from drying than is shown by those of *G. billardieri*.

Fertile fronds of *G. billardieri* with unopened ripe sporangia were collected in May 1957 and in April, July, and August 1958 in the Dandenong Ranges near Melbourne. These were sterilized by washing well in running water, then shaking for 10 min in a mixture of equal parts of a filtered solution of calcium hypochlorite (10 g : 150 c.c. water) and a 1 : 10 solution of "Savlon" in sterile water. The fronds were then washed in sterile water and allowed to dry and shed their spores between sheets of clean white paper. When the medium was not sterilized spores from washed but unsterilized fronds were used.

Spores were sown on various media—boiled roots of *Dicksonia antarctica* Labill. and boiled *Sphagnum* moss in sterile petri dishes; in porous pots filled with *Sphagnum*; on an unsterilized mossy layer from the natural habitat; and on boiled water for the early stages of germination only. Cultures were moistened with boiled water when necessary, and a deep pink solution of potassium permanganate helped to keep fungal infection in check when it occurred. Algae sometimes proved difficult to control. The porous pots became contaminated with fungi and were discarded after 4 months, the prothalli not passing the two-celled stage, though still green.

In April 1934, spores of *G. billardieri* were sown on a mineral agar, and the cultures grown for 9 months.

In May 1957, small spatulate prothalli with basal filaments still attached were found growing in the field and transferred to the laboratory on their natural substratum. These reached maturity in June 1958. Mature prothalli, some bearing young sporophytes, were also found growing in the field.

Portions of mature prothalli, some bearing an embryo, were fixed in Craf 1 or chromacetic acid (chromic acid 1 g, glacial acetic acid 8 c.c., water 800 c.c.), dehydrated by the tertiary butyl alcohol–paraffin oil method, and embedded in 52°C paraffin wax. Sections were cut at 6–8 μ, stained with iron alum haematoxylon, and counterstained with fast green and orange G. Camera lucida drawings were made of sections, and of external features of fresh and cleared material.

Fertile fronds of *C. heterophylla* collected in the Otway Forest, Vic., in November 1957 were sterilized as described for *G. billardieri*, and material collected in the Dandenong Ranges in April 1958 was washed in potassium permanganate solution for 15 min. The spores were sown on the same media as used for *G. billardieri*. As many spores were not shed from the sporangia, portions of some of the sterilized leaves were placed in boiled water in petri dishes. The dried curled leaves swelled and assumed their normal shape, the water became reddish brown, and the spores germinated and grew out from the sporangia, the prothalli forming loose masses on the surface of the leaves. Many of these small prothalli were transferred to boiled *Sphagnum* in sterile petri dishes.

C. heterophylla sporophytes growing on a mossy rock face at Tarra Valley, Vic., had young prothalli growing on the under-surface of leaves which were prostrate in the wet mossy layer. Mature prothalli, some bearing young sporelings, were also found in the moss.

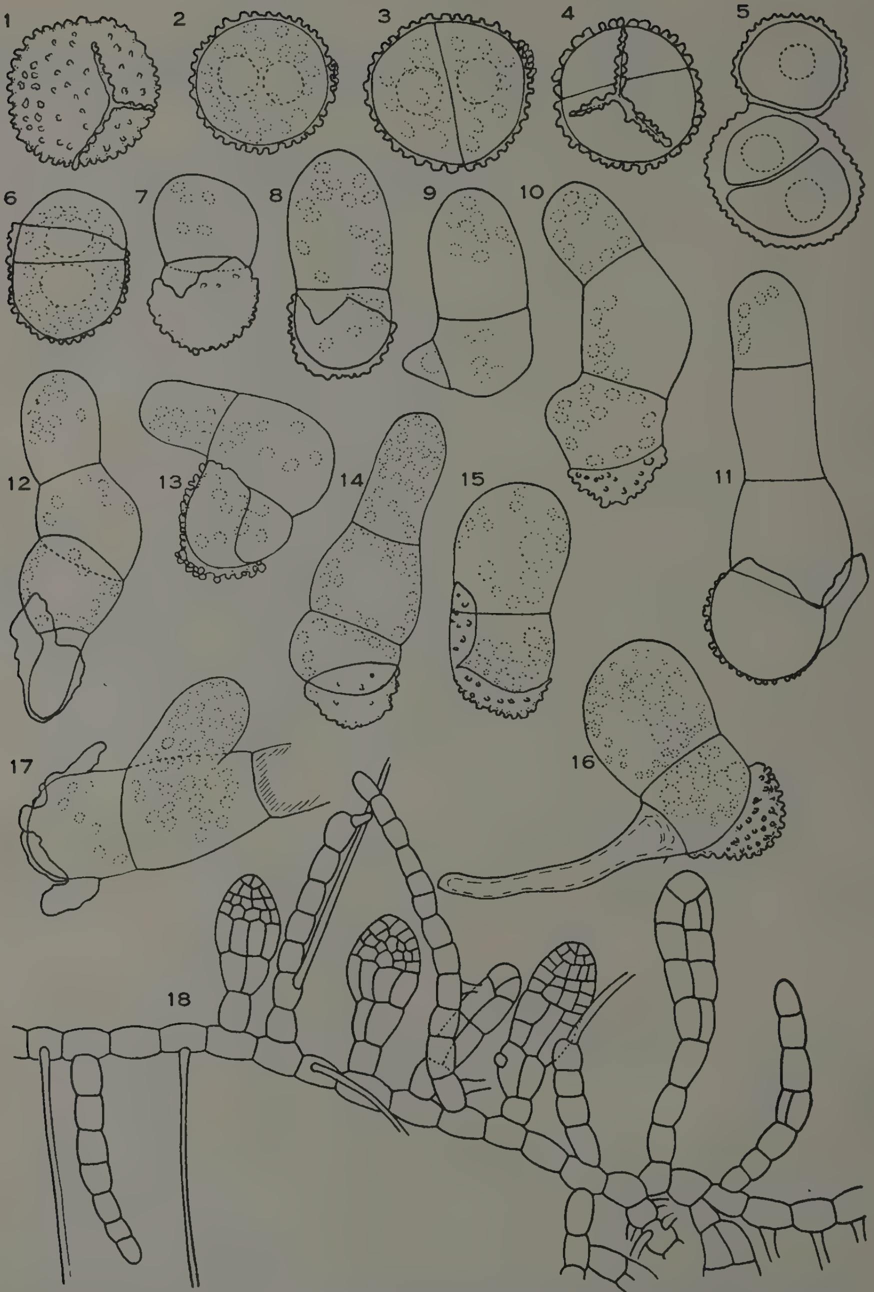
III. Spore Germination and Development of the Prothallus

The terminology applied to the spore is that used by Harris (1955).

The spores of *G. billardieri* are deep olive green, globose or sometimes tetrahedral; the thin exine is finely granular and has a triradiate tetrad scar with long laesurae (Fig. 1).

Although the spores were usually discharged in a uninucleate state, the nucleus being visible as a lighter region in the centre of the spore, it was not uncommon for spores to germinate within the sporangium before dehiscence. These spores when shed showed two cells or sometimes two nuclei but no visible dividing wall and the exine was not split (Figs. 2–4). The first wall was generally perpendicular to the axis of the spore (Fig. 3), but occasionally in the same plane (Fig. 4). Rarely, the spores were shed when incompletely separated from a tetrad (Fig. 5). The average diameter of the uninucleate spore when shed and mounted in water is about 30 μ.

The spores of *C. heterophylla* are also green, and globose to tetrahedral (Figs. 43, 44). The contact faces are sometimes flattened to concave; the laesurae are



Figs. 1–17.—Spore and early stages of gametophyte of *Grammitis billardieri*. Figs. 1–5.—Freshly shed spores. Fig. 1.—Undivided spore. ×650. Fig. 2.—Spore with two nuclei. ×650. Figs. 3, 4.—Divided spore. ×650. Fig. 5.—Two spores not separated, one showing division. ×540. Fig. 6.—Gametophyte, 4 days on boiled water. ×540. Fig. 7.—Two weeks on natural substrate. Figs. 8, 9, 11–13.—Two months on natural substrate. Fig. 10.—Seven weeks on mineral agar. Fig. 14.—Seven weeks on boiled

[*For continuation see opposite page.*]

variable, often curved (Fig. 47), and not extending to the equator of the spore (Fig. 48), or they may be quite long (Fig. 44); they are sometimes obscure, or in other cases conspicuous because of the degree of ornamentation. The exine is thin, but densely granular to papillate, the papilloid granules being easily dislodged.

There is considerable variation in the size of the spore, and germination commonly occurs while the spore is still in the sporangium. The average diameter of the undivided spore is about 45 μ, ranging from 27 to 54 μ. Spores which had divided ranged from 27 by 32 μ to 69 by 97 μ.

The spore shown in Figure 43 was dissected from a sporangium in which the annulus was tinted cream. It was pale green and densely sculptured, and the nucleus was indicated by a lighter central region. By the time the sporangia were mature and the annulus rust red the spores were nearly all dark green, binucleate or two-celled, and when shed naturally they were usually in this condition (Figs. 46–49). There were 60 spores in a sporangium. Sometimes there were 40 large dark green divided spores, several smaller uninucleate paler green spores, and some small abortive spores (Fig. 45). Occasional irregularities were seen in freshly shed spores. Figure 51 shows two divided spores which had not separated. When giant spores were present it was found that one or more of the spores from the tetrad had aborted and were left clinging to the very large spore (Fig. 50).

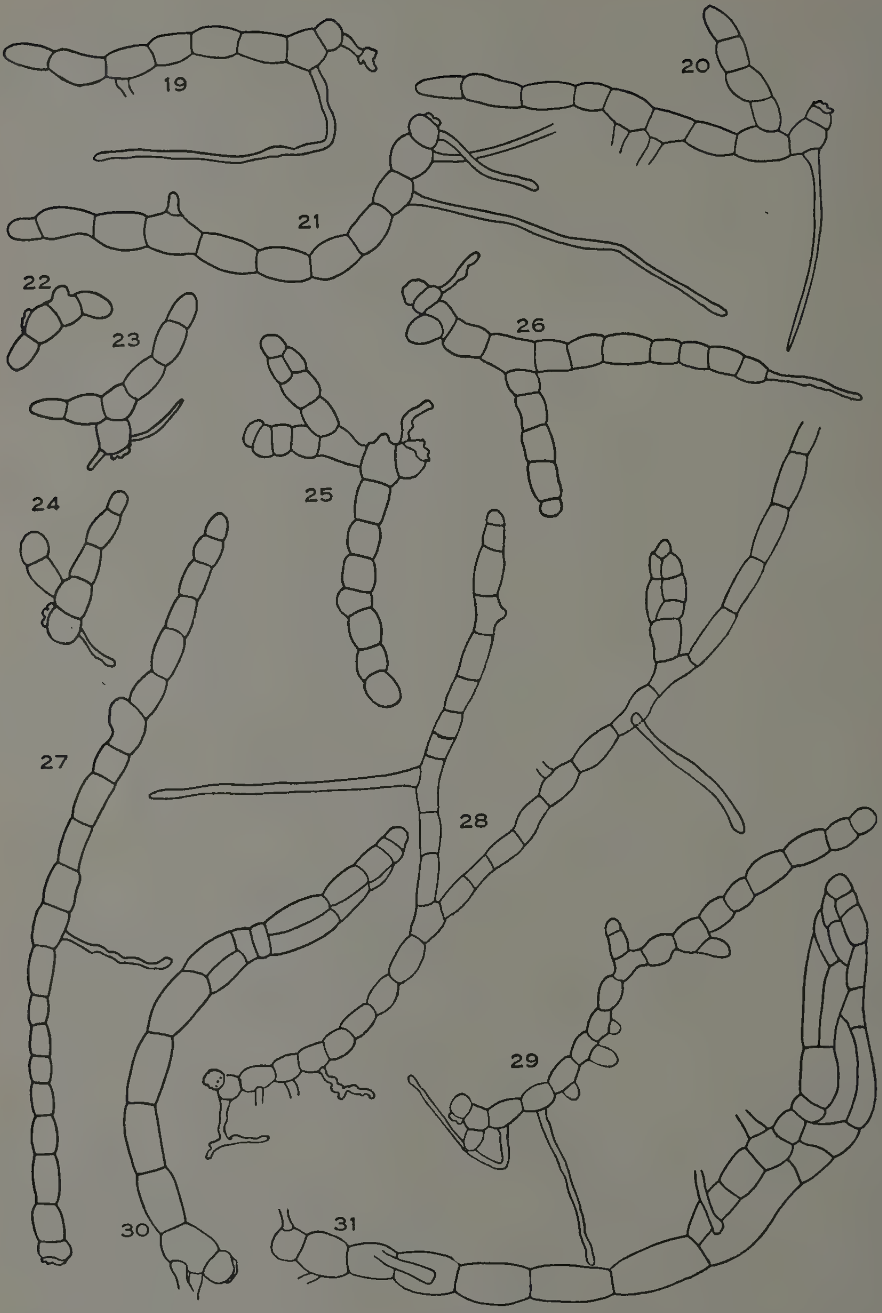
The first wall formed in the spore of *C. heterophylla* appeared to have no constant relation to the axis of symmetry, as can be seen in Figures 47–52, and thus differed from that of *G. billardieri*, where the first wall was usually transverse to the axis of the spore. The first wall often showed a curvature as indicated in Figure 50.

Germination of *G. billardieri* was the same on all media and took place early, but subsequent growth was slow. If the spore is undivided when sown, the first wall formed, before the exine splits, divides the cell into two approximately equal hemispherical cells in a similar manner to the division which occurs so often in the sporangium. Figures 6–16 show stages in germination. The exine often split in 3 to 4 days (Fig. 6), but the prothallus sometimes stayed at the two-celled stage for many months. The exine split at the triradiate ridge and usually adhered to the proximal or basal cell for a considerable time. The distal cell protruded from the exine and a uniseriate filament of short cells formed. The three-celled stage was reached in 7 weeks.

Rhizoid development is generally delayed and in the majority of cases no rhizoid appears until the filament is three or four cells, sometimes more. The first rhizoid frequently arises from the basal cell, in the majority of cases from the side (Figs. 9, 10, 16) but occasionally from the proximal pole, pushing the exine off (Fig. 12). It is short and at first has a few pale chloroplasts which soon disappear, and it turns brown early. The basal cell remains short and bulbous with exine persistent, and may produce a second and third rhizoid later (Figs. 23, 42).

Figs. 1–18 (*Continued*)

water. Figs. 15, 16.—Germinated in ruptured sporangium, 6 months. Fig. 17.—Main filament injured, new branch from second cell. Figs. 7–17 ×435. Fig. 18.—Eleven months on boiled *Sphagnum*, plates developing from branching filament. ×75.



Figs. 19–29.—Filamentous stage of gametophyte of *G. billardieri*. Figs. 19–21.—Prothallus after 5 months on boiled *Dicksonia* roots. ×115. Figs. 22–24.—Two months on agar. ×115. Figs. 25–27.—Six months on agar. ×115. Figs. 28, 29.—Three months on water, then transferred to boiled *Dicksonia* roots for 9 months. ×75. Fig. 30.—Longitudinal divisions, 10 months on boiled *Dicksonia* roots. ×120. Fig. 31.—Apical cell, 10 months. ×120.

The filament may develop from the side instead of the tip of the second cell (Fig. 13) and this possibly occurs when the first wall forms in a plane parallel to the axis of the spore.

Figures 19–29 show the variability of the filamentous stage. After 5 months on all media except water, the filaments were long and sometimes branched, consisting of short cells, with rhizoids either long or very short. The long rhizoids were slender, straight, and brown with hyaline tips. Rhizoids occasionally branched on contact with the substratum (Fig. 28) but these were readily torn off.

The prolonged filamentous stage appears to be inherent, and not induced by unfavourable conditions, though possibly related to the mossy situations in which the spore germinates in nature. A few alien prothalli in the cultures became cordate and matured in a few weeks.

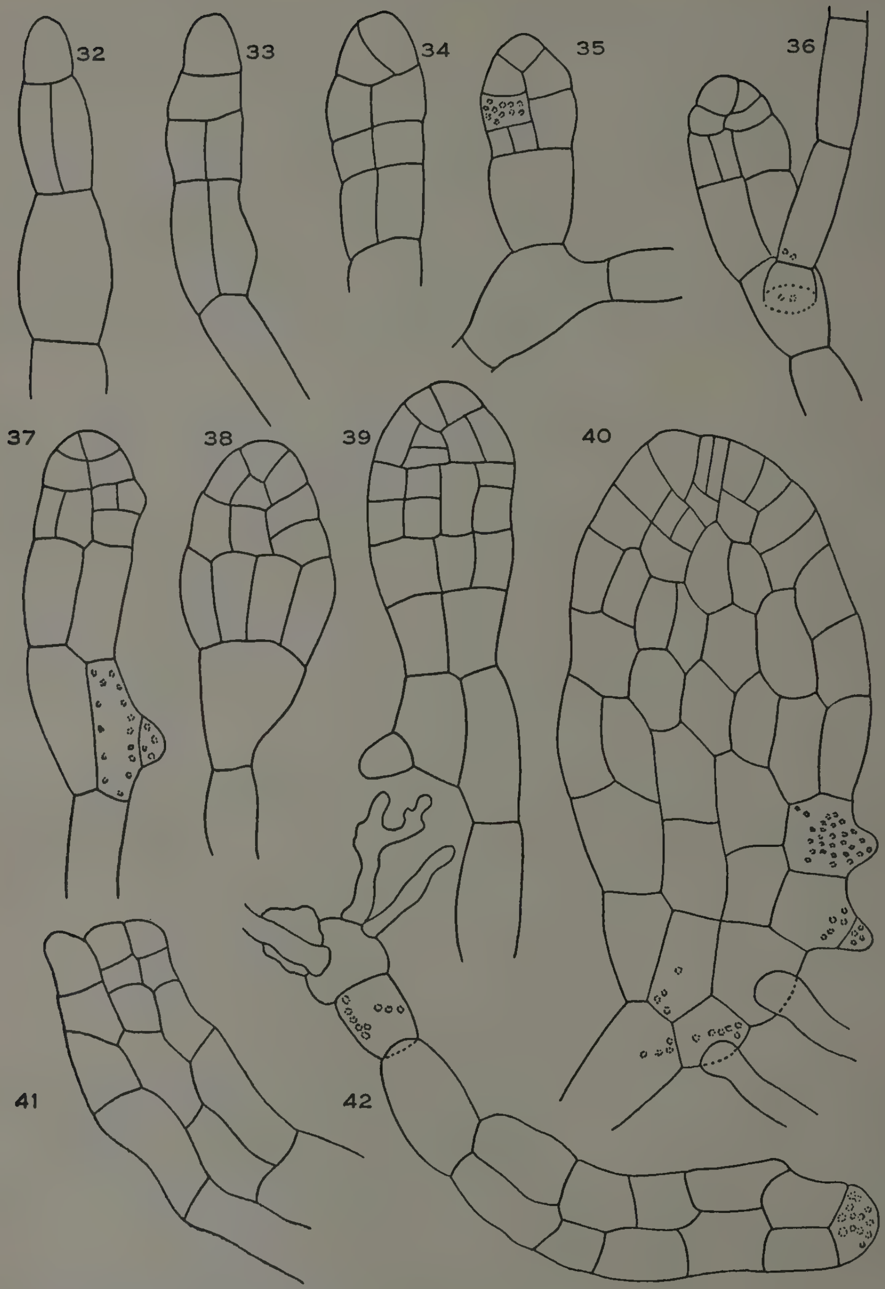
In cultures on boiled *Dicksonia* roots, filaments were found to be expanding to spatulate plates at 6–10 months. Figures 30–42 show stages in plate development. The first longitudinal division occurred two or three cells back from the tip (Figs. 32, 33), later divisions took place in cells further back, and the number of undivided cells at the base of a plate varied considerably. Occasionally as few as three cells remained undivided (Fig. 42), but usually more of the filament cells were left at the base (Figs. 30, 31), and the portion of a prothallus shown in Figure 40 had a 16-celled basal filament. Divisions also occurred in cells nearer the apex, and the terminal cell divided obliquely to form a wedge-shaped apical cell (Figs. 34–36). In some cases longitudinal and transverse divisions produced a marginal meristem and no special apical cell was formed (Fig. 41).

Plate formation took place in many of the filaments on boiled *Dicksonia* roots, occurring particularly in the regions where the roots were contaminated by fungi. The prothalli were more vigorous in these regions and although no experiments have been made to check this, it seems possible that the fungi stimulated the prothalli to plate formation, possibly by enriching the substrate. Hutchinson and Fahim (1958) reported stimulation of prothallial growth by fungi.

The spatulate prothalli developed marginal rhizoids (Figs. 37, 39, 40), and the walls of the cells perpendicular to the surface were pitted. Pitted walls are shown in Figure 132 and Plate 2, Figure 1.

Prothalli were transferred from sterile water to boiled *Dicksonia* roots, and in many cases the original short-celled filament grew along the surface of the substrate to which it was attached by rhizoids, and sent up aerial filaments with longer cells from which flattened plates were produced (Figs. 28, 29). This type of development was common in cultures on boiled *Sphagnum* (Fig. 18), and was also found to occur in the field (Fig. 79*A*, *B*). It may take place when there are some adverse elements in the environment.

Germination stages of *C. heterophylla* after 2 weeks on boiled water are shown in Figures 53–57. Many spores had not passed the two-celled stage, some had split the exine, and others had advanced to a three-celled filament. The first division, though it usually divides the spore into two approximately equal hemispheres, is not constant in its relation to the axis of the spore, and the young prothalli are not as uniform in their appearance as those of *G. billardieri*. If the first division



Figs. 32–42.—Stages in plate formation of gametophyte of *G. billardieri.* ×210. Fig. 32.—First longitudinal division. Fig. 34.—Oblique division in terminal cell. Fig. 35.—Apical cell formed. Fig. 40.—Spatulate prothallus showing stages in development of marginal rhizoids. Fig. 41.—Longitudinal and transverse divisions, no apical cell, 10 months on boiled *Dicksonia* roots. Fig. 42.—Prothallus with an unusually short filament, branched rhizoid.

is perpendicular to the polar axis the filament grows out in a straight line (Fig. 59), but if the first wall is at some other angle the second division is not parallel to the first, and the filament does not grow from the tip of the second prothallial cell but from a lateral position as in Figures 55 and 60.

Figures 58 and 59 show filaments grown for 6 weeks on boiled *Sphagnum*. Many had reached 10 cells, and by 3 months some filaments were 15–20 cells and branched (Figs. 70, 71); others had only two cells and some had not split the exine. Prothalli grown on boiled water had narrower filaments (Fig. 60) and did not progress beyond eight cells.

Rhizoids did not often form early, and appeared after a few cells of the filament had formed. They were not generally produced from the basal cell, which remained more completely encased in the spore coat than in *G. billardieri*, although occasionally an irregular tear appeared in the exine and a rhizoid protruded from the basal cell (Figs. 65, 70, 76). They showed a stronger tendency to branch on contact with other objects and act as attaching organs than was the case with those of *G. billardieri*. Figure 66 shows a rhizoid clasping another prothallus. This was fairly common where spores germinated in a sporangium.

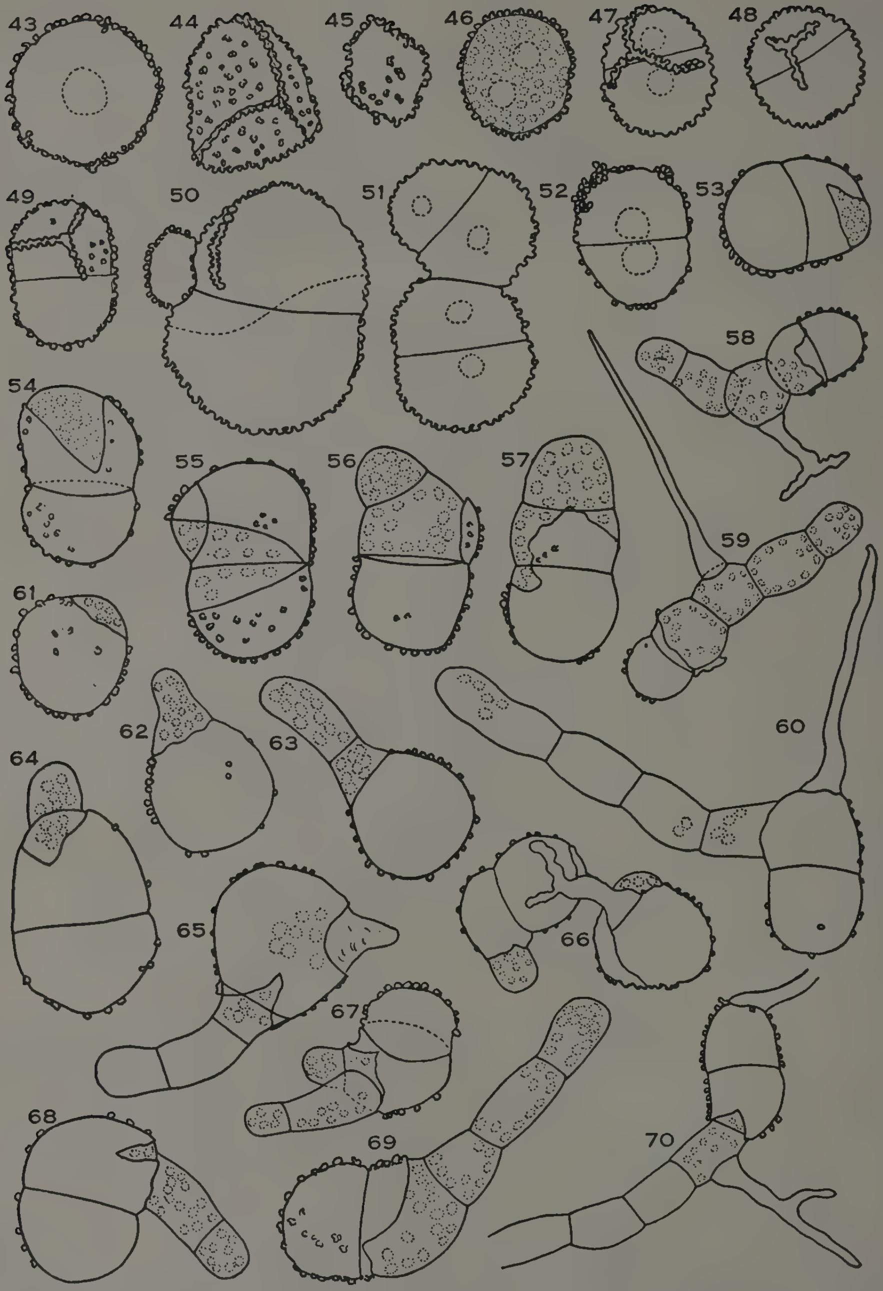
The rhizoids are broad at their point of attachment to the prothallial cell and are colourless in this region, whereas the rest of the rhizoid is brown. The few chloroplasts present in young rhizoids soon disappear.

Dehiscence of spores from sporangia was rarely complete, and spores germinated in ruptured sporangia on fronds placed in boiled water. The prothalli grew out and appeared as a mass of filaments on the leaf. They had a less robust germ tube, advanced more slowly than those which had more space on the various media, and showed more irregularities, although they were very green and healthy (Figs. 61–69). In some cases a type of germination not seen in *G. billardieri* was observed. The exine burst before the first division took place, as is usual, and a smaller cell was cut off from the protrusion (Figs. 61–63). Prothalli were also observed where two germ tubes were put out by the second prothallial cell (Figs. 67, 74).

Other conditions being equal, prothalli produced from larger spores usually had larger cells than those from smaller spores (Figs. 72, 73). The magnification of Figure 72 is only two-thirds that of Figure 73. The rhizoid of the large-celled prothallus in Figure 73 is clasping a normal-celled filament. Giant spores were rare, but the few prothalli produced from them had very large cells well filled with chloroplasts of normal size (Fig. 73). Such prothalli became branching filaments but were not seen to broaden to a plate in 9 months.

Longitudinal divisions appeared in the filaments, and many of the prothalli were spatulate and with marginal rhizoids at 3 months (Figs. 75–77). As with *G. billardieri* the first longitudinal division usually occurred a few cells back from the tip (Fig. 75), and the cell walls perpendicular to the surface of the prothallus became pitted.

Figure 76 shows a prothallus at the early plate stage with a basal filament of six cells. It had rhizoids which were long and branched at the tip.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Figs. 43–70.—Spores and early stages of gametophyte of *Ctenopteris heterophylla*. Fig. 43.—Spore dissected from immature sporangium. ×435. Figs. 44–52.—Freshly shed spores. Fig. 44.—External view. ×435. Fig. 45.—Abortive spore. ×435. Fig. 46.—Spore with two nuclei. ×325. Figs. 47–49, 52.—Spores showing first division. ×325. Fig. 50.—Giant spore with abortive spore attached. ×325. Fig. 51.—Two divided

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Figure 77 shows the top portion of a prothallus with an apical cell. It had a basal filament of 12 cells with six long branched rhizoids.

At 9 months the prothalli were elongated and ribbon-like with a slightly indented apex and marginal rhizoids. Unfortunately further development was not observed as the cultures died in the extreme heat during the summer.

G. billardieri gametophytes at the spatulate stage and estimated to be a year old were found in the forest in May 1957 and kept in the laboratory on their natural substratum. They became elongated and ribbon-like with a slightly indented apex and marginal rhizoids. After 12 months, divisions parallel to the surface formed in some of the cells behind the notched apex, and discontinuous axial cushions two to three cells thick were produced throughout the winter and spring (Fig. 80).

Brown rhizoids were in discontinuous groups, and practically confined to the margin arising from the edge or sometimes the under-surface of marginal and submarginal cells (Fig. 88), but in older portions of the prothalli were occasionally formed in large numbers on the wings. Rarely were any seen on the cushion region as reported by Goebel (1888) for *Ctenopteris obliquata*.

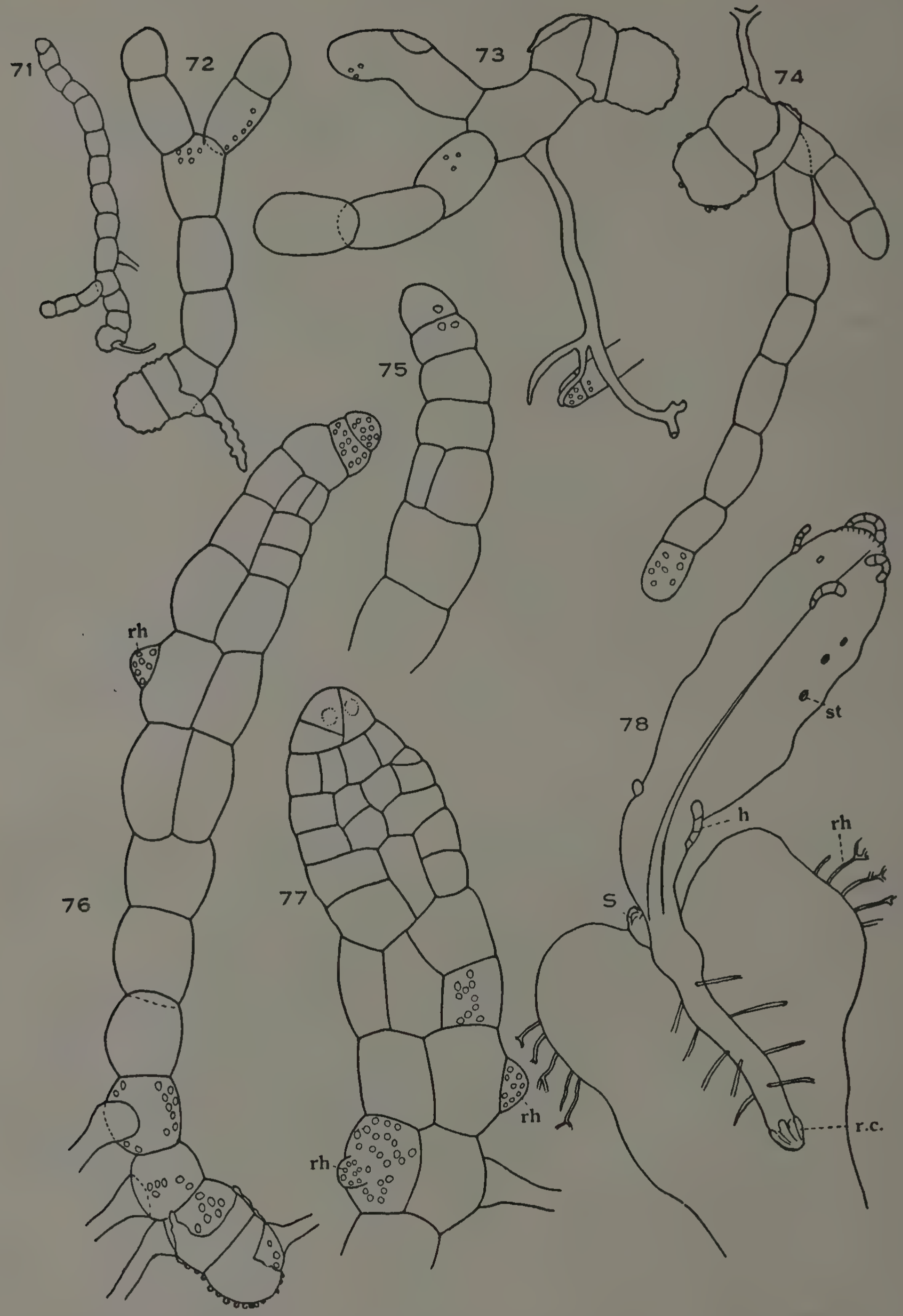
Mature prothalli found in the field showed more irregularities than those grown to maturity in the laboratory. Figure 81 shows a prothallus with sex organs and an embryo, though the apex is still spatulate with no indentation. Others exhibited irregular branching (Figs. 83, 84), and a few in which fertilization had evidently occurred soon after maturity was attained were much less elongated (Fig. 86). The majority, however, were of the type grown in the laboratory.

IV. Hairs

Hairs were produced by the prothalli of *G. billardieri* when cushion development began, and were a conspicuous and characteristic feature of the gametophyte. These hairs were spine-like, and developed on the margin of the prothallus in the region of the notch, attaining a length of about 0·25 mm (Fig. 93). Each arose from a wedge-shaped initial cell, which was produced by the division of a marginal cell in which an oblique wall was formed between the outer marginal wall and the wall nearest the apex, as in Figures 90 and 91. This initial cell contained a few chloroplasts, and grew out to form a long tapering unicellular hair which was usually curved towards the apex of the prothallus. The hairs frequently appeared to be formed in acropetal succession, but it was not uncommon for a young hair to develop between older ones. Figure 98 shows the anterior margin of a prothallus with developing hairs. A few hairs divided into two cells by either an oblique or a transverse wall (Figs. 96, 97).

Figs. 43–70 (*Continued*)

spores, not separated. ×325. Figs. 53–57.—Germination, 14 days on boiled water. ×325. Figs. 58, 59.—Six weeks on boiled *Sphagnum*. ×210. Fig. 60.—Seven weeks on boiled water. ×285. Figs. 61–69.—Germinated in ruptured sporangium, 3 months. Figs. 61–63, 65.—Irregular type of germination. Fig. 66.—Branched rhizoid clasping a prothallus. Fig. 67.—Two germ tubes. Figs. 61, 66, 67 ×285. Figs. 62–65, 68, 69 ×325. Fig. 70.—Portion of 15-celled filament, 3 months on boiled *Sphagnum*. ×210.



Figs. 71–77.—Filaments and plate formation in *C. heterophylla*. *rh*, Rhizoid. Figs. 71–73.—Branched filaments, 3 months on boiled *Sphagnum*. Fig. 71 ×75. Fig. 72 ×210. Fig. 73.—Prothallus from giant spore with branched rhizoid clasping normal filament. ×140. Fig. 74.—Prothallus with two filaments germinated in ruptured sporangium, 3 months. Fig. 75.—First longitudinal division in filament. Fig. 77.—Prothallus showing apical cell. Figs. 72, 74–77 ×210. Fig. 78.—Prothallus of *C. heterophylla* found in the field. Young sporeling attached. *S*, stem; *h*, hair; *st*, stoma; *r.c.*, root cap. ×c. 17.

On the older parts of prothalli which had several cushion regions, rhizoids were sometimes seen interspersed with hairs, and, rarely, a rhizoid arose from a cell which already bore a hair (Fig. 94).

In old hairs the chloroplasts disappeared and the walls became thick and light brown, the basal wall pitted (Fig. 95).

The development of hairs was by no means uniform and whereas they were prolific on some prothalli, appearing on almost every cell at the anterior margin (Fig. 93), they were quite scarce on others, and one though bearing sex organs had none.

Occasionally a hair shows a deviation from the normal mode of development, and some arose from the side of the cell away from the apex instead of from the side nearer the apex (Fig. 93).

The hairs were confined to the margin, none being seen on either the dorsal or the ventral surface. Goebel (1888, 1905) reported similar thick-walled brown bristle hairs on the margin of the gametophyte of *Ctenopteris obliquata*.

One prothallus found in the field bore some unusual hairs (Fig. 99*A*, *B*). It had produced two two-celled hairs with glandular tips, and one three-celled hair with a glandular tip and a spine-like branch like those found on the young sporeling. These were formed on the margin a short distance from the apex, and interspersed with the normal spine-like type of hair (Figs. 102, 103).

Figures 100 and 101 show types of hairs found on sporeling leaves.

The prothallus also bore four antheridia on a narrow cushion just back from the apex. This unusual prothallus was found in a locality where a broader-leaved type of sporophyte was abundant.

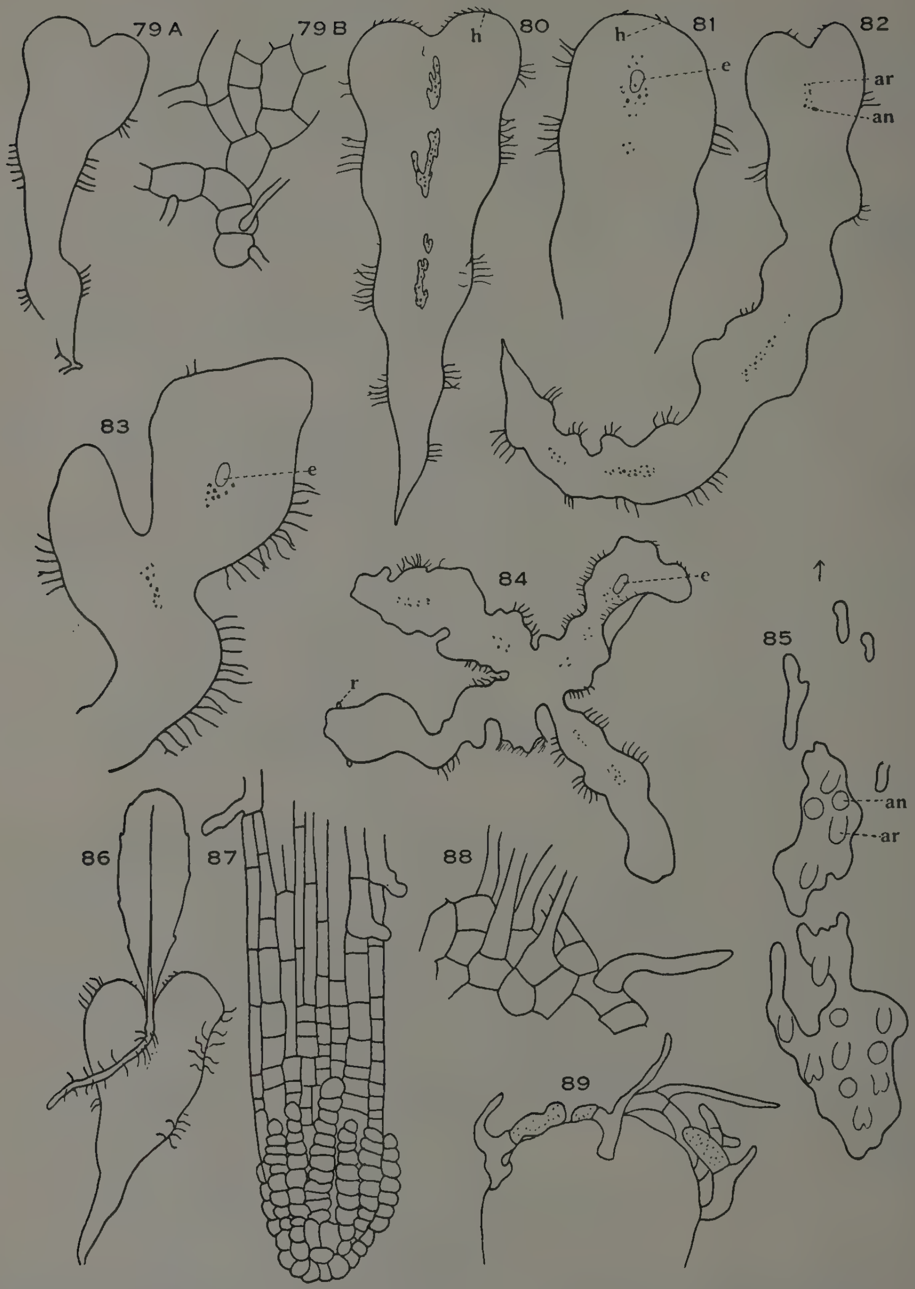
A few mature prothalli of *C. heterophylla* were found in the field in two localities. Evidence obtained from these indicated that the prothallus is very similar to that of *G. billardieri*, with a thin discontinuous cushion bearing archegonia and antheridia together. On none of these prothalli was there any evidence of the distinctive hairs borne by the gametophyte of *G. billardieri* and reported by Goebel (1888, 1905) for *C. obliquata*. This does not rule out the possibility that hairs may occur on the prothallus of *C. heterophylla*, as several prothalli of *G. billardieri* were observed to have few hairs and one had no hairs.

The hairs on sporelings of *C. heterophylla* (Fig. 78) differed from those on sporelings of *G. billardieri*, and were multicellular and uniseriate with no spine-like branch.

V. Reproductive Organs

(*a*) *Antheridia*

The antheridia of *G. billardieri* were formed at an unusual stage in the development of the prothallus and were rarely prolific. Instead of appearing before, they arose after several archegonia had formed and were produced on the ventral side of the thin cushions, interspersed with and in close proximity to the archegonia (Fig. 85). They were seen neither on the wings nor on the margins but were occasionally found on the dorsal surface in the cushion region. Antheridia were



Figs. 79–89.—Gametophytes of *G. billardieri*, ventral surface. Figs. 79*A*, *B*.—*A*, prothallus attached to basal filament, found in the field. ×*c*. 14. *B*, enlarged base of *A*. ×110. Figs. 80–84.—Mature prothalli. *ar*, Archegonium; *an*, antheridium; *r*, regeneration; *e*, embryo. Fig. 80.—Prothallus grown 2 years on natural substrate. ×*c*. 8. Fig. 81.—Prothallus with spatulate apex and bearing an embryo, found in the field. ×*c*. 10. Fig. 82.—Very elongated prothallus. ×*c*. 8. Fig. 83.—Portion of branched prothallus with embryo, found in the

[*For continuation see opposite page.*]

difficult to distinguish from the archegonia with a lens, and the wall cells were rich in chloroplasts, so that the number and disposition of cells were not easily determined in fresh material.

The antheridia showed some variation in size and complexity but were generally slightly more complex than is usual in the higher ferns.

The antheridium arises from a wedge-shaped initial cell cut off by an oblique wall from a superficial cell (Fig. 104). This initial cell divides into two by a wall parallel to the first or basal wall, forming an inner or basal cell and an outer cell (Fig. 105), or occasionally by a wall more or less perpendicular to the basal wall (Fig. 106). Further divisions delimit the wall cells from the androgonial tissue, which reaches to the basal wall in mature antheridia. In most cases the cap cell is divided (Figs. 110*A–C*, 116), and the wall of an antheridium at maturity has five or six nuclei. The number of sperms in median longitudinal section varies from 12 to 25 but is usually about 15.

Figure 107 shows a section in which the antheridium has been cut obliquely. A dome-shaped wall has delimited the androgonial cell, whose nucleus has divided, and the nucleus of the outer cell is dividing prior to the formation of the ring and cap cell.

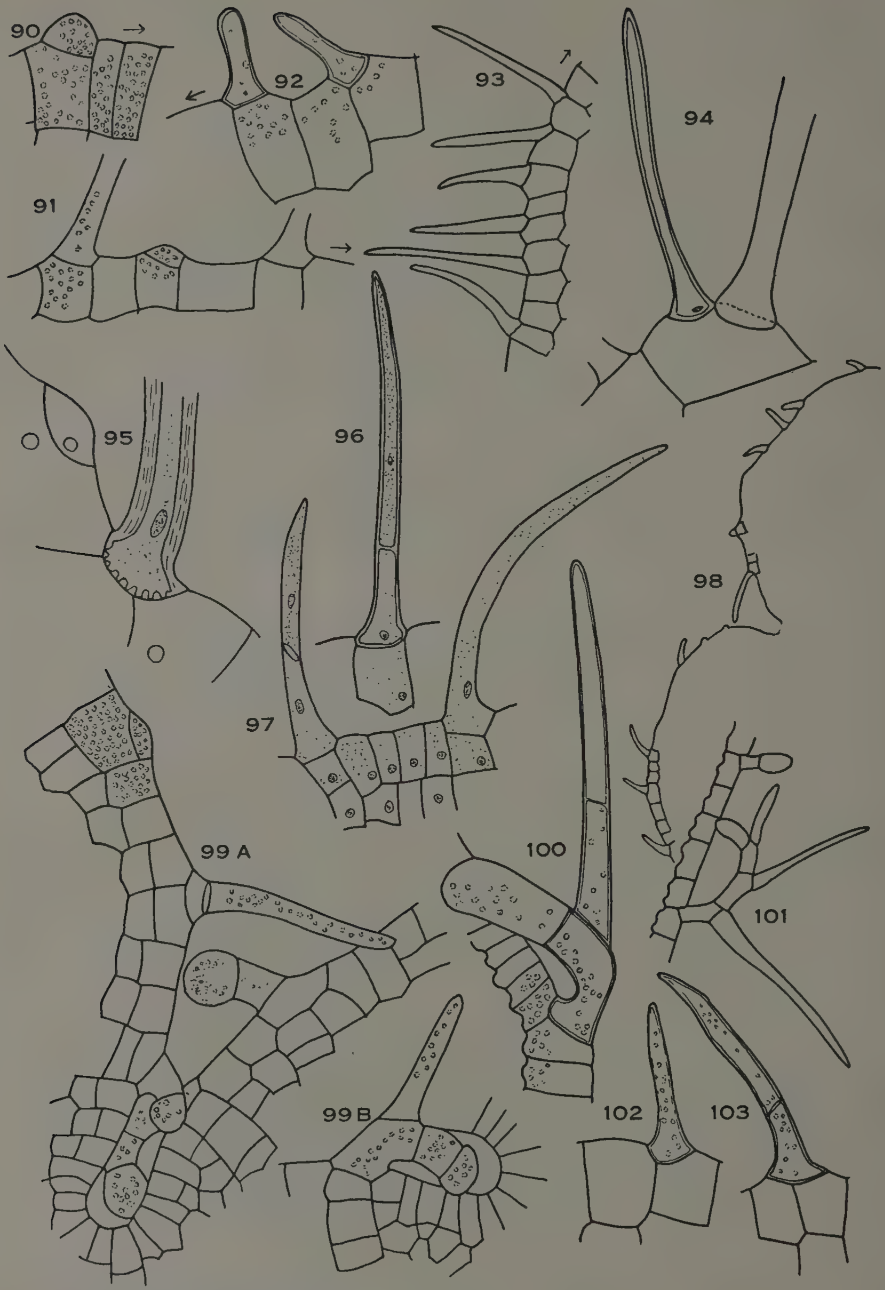
Figure 109*A–C* shows the first, fourth, and fifth sections of an antheridium, showing the first division of the androgonial cell and the ring and cap cells formed. The basal cell has divided into two by a wall perpendicular to the basal wall. A divided basal cell or two basal cells were often observed in sections of immature antheridia (Figs. 108, 109).

It appears from sections of several mature antheridia that, although the nucleus divides, the division of the basal cell is not always complete as shown in Figure 110*A–D*. This condition is also indicated by Plate 1, Figure 1, which shows the two nuclei and dividing wall in the basal cell, and Figure 112*A*, *B*, which shows consecutive sections of the same antheridium—*A* the median, *B* the basal cell without any dividing wall. This connecting wall shows a resemblance to the "binding wall" found in the lower ring cell of antheridia of the Cyatheaceae (Stephenson 1907; Stokey 1930).

It is possible that as the androgonial tissue develops it pushes downwards and comes in contact with the basal wall of the antheridium in the central region, before or after complete or partial division of the basal cell. This apparent incomplete division of the basal cell may not be real, as it is possible that a wall in the same plane as that of the sections would be unrecognizable. Unfortunately transverse sections, which may have clarified the position, were not made.

Figs. 79–89 (*Continued*)

field. ×*c*. 14. Fig. 84.—Branched prothallus, lower part necrosed, showing discontinuous cushions, embryo, and regenerations. ×*c*. 8. Fig. 85.—Discontinuous cushion of a prothallus, showing archegonia and antheridia. Arrow points towards the apex. ×49. Fig. 86.—Prothallus with young sporeling. ×*c*. 8. Fig. 87.—Tip of first root with root cap. ×95. Fig. 88.—Rhizoids from under-surface of cells at margin of prothallus. ×75. Fig. 89.—Apex of young cotyledon showing hairs. ×75.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Figs. 90–103.—Hairs of *G. billardieri*. Fig. 90.—Young hair cell, near apex. ×285. Fig. 91.—Hair initial, between older hairs. ×210. Fig. 92.—Young hairs. ×210. Fig. 93.—Prolific development of hairs on anterior margin of prothallus. ×75. Fig. 94.—Rhizoid on same cell as hair, on older portion of thallus. ×210. Fig. 95.—Lower por-

[*For continuation see opposite page.*]

Davie (1951) describes a divided basal cell in *Cyclosorus parasitica* (L.) Farwell, and Stokey and Atkinson (1954*b*) illustrate a divided basal cell as an irregularity in the antheridium of *Didymochlaena sinuata* Desv., but in these cases division was complete and there was no penetration of the androgonial tissue to the basal wall.

In the antheridium shown in Figure 113 the nucleus of the basal cell had not divided but appeared in an active condition, and there were two ring cells and a divided cap cell.

Sections of more complex mature antheridia are shown in Figures 111*A–D*, 114, and 115 (not median).

Ameristic male prothalli were not produced, and although the filamentous stage of the gametophyte is very prolonged no development of antheridia occurred on these filaments.

(*b*) *Archegonia*

Archegonia appeared on prothalli when they were about 2 years old, borne on the ventral surface of the midrib, which was always thin—usually two cells thick, but occasionally three on vigorous prothalli—and discontinuous. Sometimes small scattered patches only one or two cells in extent bore single archegonia.

The initial cell of an archegonium usually appeared 12 to 16 cells back from the apex, a greater distance than is usual in most fern prothalli. Young archegonia formed in acropetal succession on the youngest cushion, which was nearest the apex (Fig. 117). Occasionally young archegonia and antheridia developed among old archegonia on the older cushions further back on the prothallus. Some of these older prothalli bore more than 50 archegonia and about 16 antheridia.

The archegonium develops in the normal manner, as shown in Figures 118–126, but it was not uncommon to find a wedge-shaped central cell, as seen in Figure 117.

The apex of the prothallus was always in the plane of the wall formed by the first division of the primary neck cell, as illustrated by Figure 134. There are usually only four cells in each tier of the neck when the axial row is completed (Fig. 132); but the neck cells continue to increase in number and elongate more on the anterior side, so that at maturity the archegonial neck is curved towards the posterior end of the prothallus. The neck of the mature archegonium is frequently longer than is usual in the higher ferns, with five to eight cells on the long side of the neck and four to six cells on the short side, and the lower cells may divide longitudinally or obliquely (Figs. 127–129). The neck canal cell is not often

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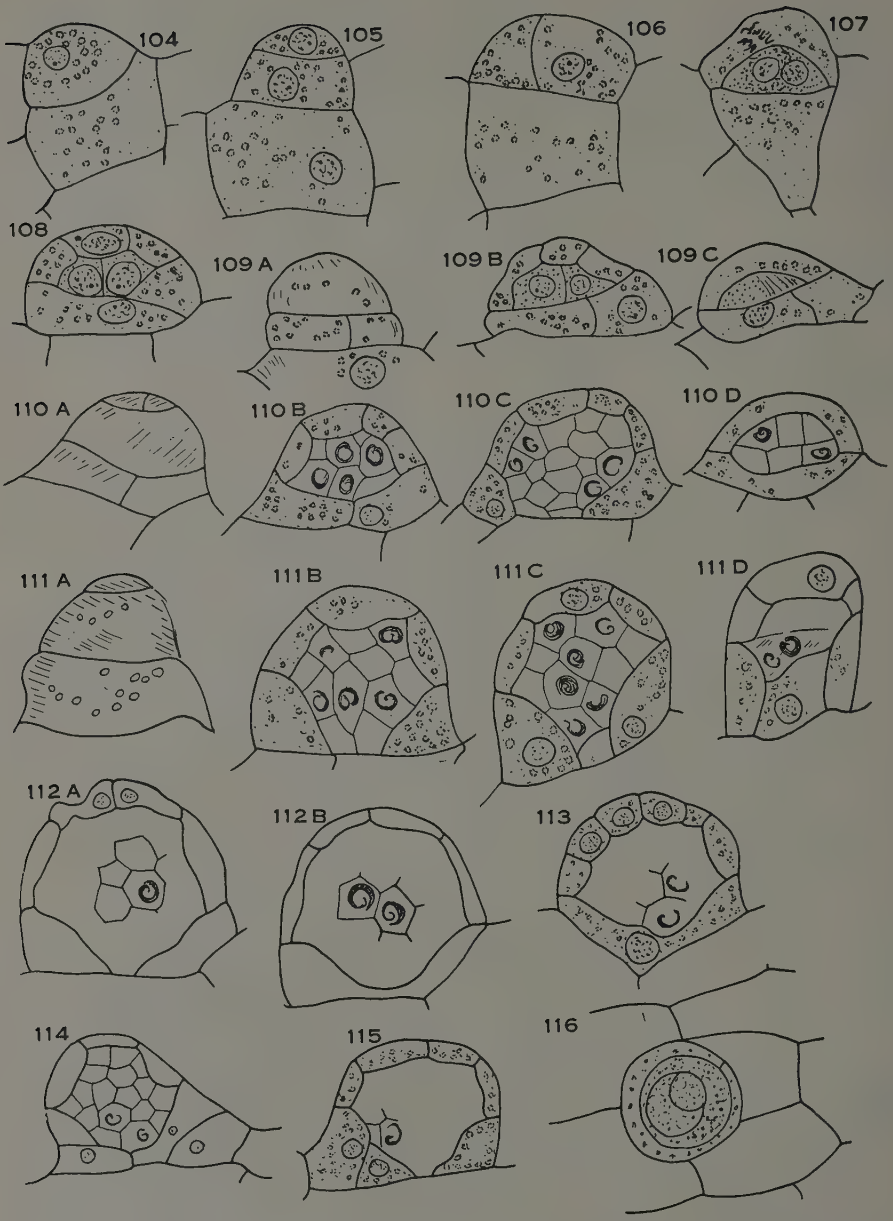
Figs. 90–103 (*Continued*)

tion of old hair with thick walls and pitted basal wall. Cleared. ×355. Figs. 96, 97.—Two celled hairs, cleared. ×210. Fig. 98.—Anterior region of mature prothallus, showing hairs. ×49. Fig. 99*A*, *B*.—*A*, apex of unusual prothallus with glandular hairs, a wedge-shaped hair initial, and normal spine-like hairs. *B*, ventral view of glandular hair, with spine-like branch, near the apex of the prothallus. ×210. Fig. 100.—Sporophytic hairs on leaf margin of young sporeling. ×210. Fig. 101.—Sporophytic hairs on leaf margin. ×75. Figs. 102, 103.—Hairs from same thallus as Fig. 99. ×210.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Figs. 104–115.—Longitudinal sections of antheridia of *G. billardieri*, ventral surface up. Fig. 104.—Antheridial initial cell. ×435. Fig. 105.—First division of antheridial initial. ×435. Fig. 106.—Same. ×540. Fig. 107.—Oblique section of young antheridium. × 540. Fig. 108.—Immature antheridium. ×435. Fig. 109*A–C*.—Three sections (*B*, *C* consecutive) of an immature antheridium with divided basal cell. ×435. Fig. 110*A–D*.—Sections of a typical mature antheridium, *A–C* consecutive. ×355. Fig. 111*A–D*.—Alternate sections of a more complex mature antheridium. ×435. Fig. 112*A*, *B*.—

[*For continuation see opposite page.*]

as bulbous at the tip as is usually reported for the advanced ferns. Sometimes the two neck canal nuclei are separated by a wall (Fig. 130).

The basal cell frequently divides longitudinally or transversely or both (Figs. 131, 132), and this may occur at an early stage (Fig. 131), but the jacket layer develops after the axial row is completed and final development is taking place (Figs. 128, 129).

When the archegonium dehisces there is a forcible expulsion of the contents of the neck, leaving a passage clear to the ovum as described by Ward (1954*a*) in *Phlebodium aureum* J.Sm. Similar forcible expulsion has been noted by the author in archegonia of *Mecodium australe* (Willd.) Copel., a member of the Hymenophyllaceae.

As mentioned earlier, the antheridia appear after several archegonia have developed and are in close proximity to them. It is probable that antheridia appear if cross fertilization fails, and self-fertilization may then take place. Some prothalli found in the field bore archegonia only and these showed a developing embryo. As a rule there were large numbers of archegonia with fewer interspersed antheridia. Embryos borne on gametophytes in the cultures were all self-fertilized, as the prothalli were widely separated on the substratum.

Sections of a prothallus which had been flooded with water before fixation showed sperms in the neck of an open archegonium, and a trail of sperms from a dehisced antheridium on the same prothallus.

VI. Embryo

Embryos of *G. billardieri* were found in the field and also appeared on prothalli in culture in the laboratory. At no time was more than one embryo seen on a prothallus. The most conspicuous features of the embryo were the very large cells of the foot region, some being more than 50 μ in length, and the extremely thin cushion on which the embryo was borne.

Sagittal sections of prothalli bearing embryos of different ages were made.

Figure 133 shows telophase of the first division of the fertilized ovum. The basal wall is parallel to the axis of the archegonium and transverse to the axis of growth of the prothallus, as is usual in leptosporangiate ferns, and the epibasal or anterior cell is smaller than the hypobasal cell.

Plate 2, Figure 1, is a section of an embryo which has not burst from the calyptra. The cotyledon, root, and stem regions are defined and the foot region is conspicuous for its extremely large vacuolated cells, which penetrate between the cells of the jacket layer.

Figs. 104–116 (*Continued*)

Consecutive sections of the same antheridium as illustrated in Plate 1, Fig. 1. ×435. Fig. 113.—Longitudinal section (not median), of a mature antheridium with an undivided basal cell, two ring cells, and a divided cap cell. ×435. Fig. 114.—Longitudinal section (not median), of a more complex mature antheridium. ×285. Fig. 115.—Complex antheridium. ×435. Fig. 116.—Surface view of antheridium. ×285.

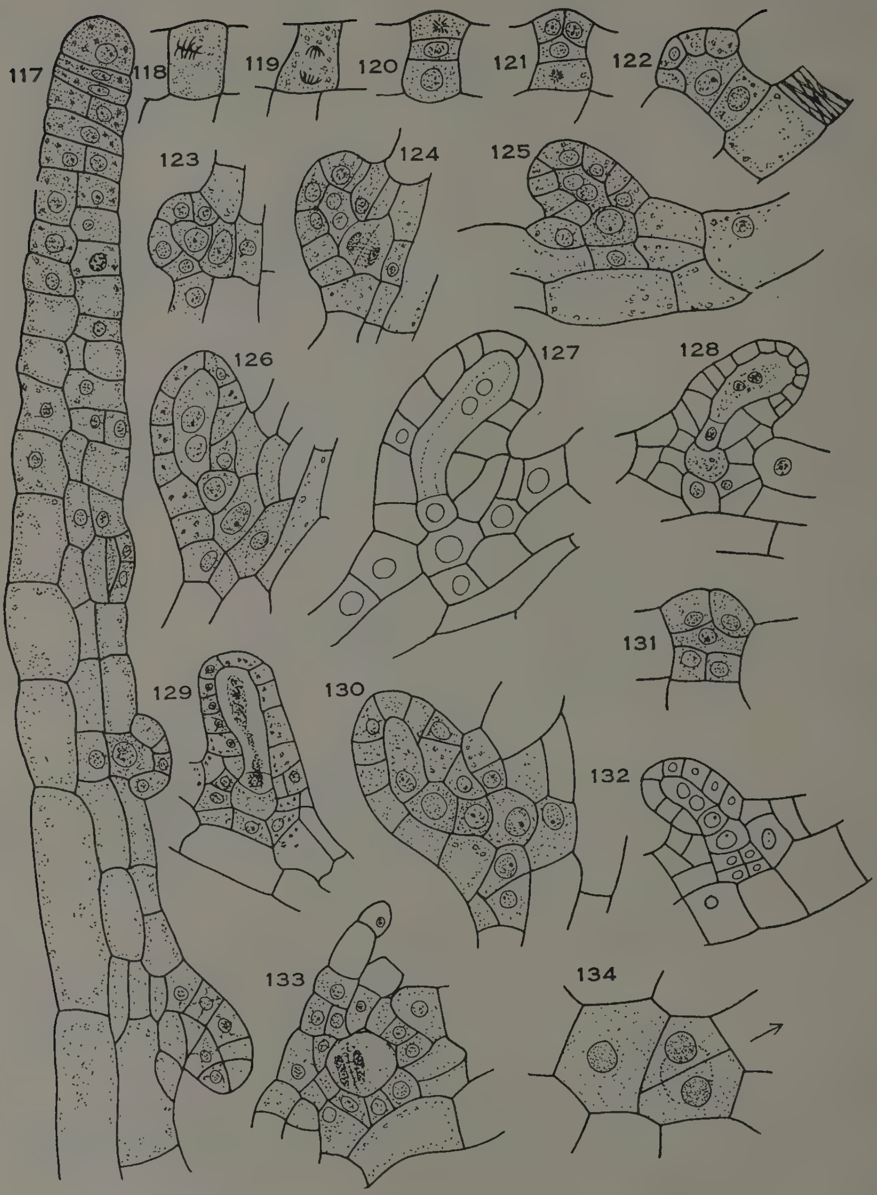


Fig. 117.—Longitudinal section of apex of mature prothallus, showing thin cushion and young archegonia. ×210. Figs. 118–133.—Longitudinal sections of archegonia of *G. billardieri*, ventral surface up. Figs. 118–127.—Stages in development. ×285. Fig. 122.—Shows pitting in lateral wall of prothallus. Figs. 126–129.—Mature archegonia, Figs. 128, 129 with long necks. ×210. Fig. 130.—Anomalous archegonium, with two neck canal cells. ×285. Fig. 131.—Early division of basal cell. ×285. Fig. 132.—Mature archegonium, basal cell divided into four cells. ×210. Fig. 133.—Telophase of first division of fertilized ovum, posterior half larger. ×210. Fig. 134.—Surface view of young archegonium, showing first division of the primary neck cell. ×435.

Plate 2, Figure 2, shows a section of a more advanced embryo in which the cotyledon and root have broken from the calyptra.

There is a development of rudimentary vascular tissue between cotyledon, root, and stem. The foot region is still composed of large haustorial type cells and there is only one layer of prothallial cells beneath the embryo. The cotyledon had developed glandular hairs and did not show circinate vernation.

Figure 86 shows a young sporeling attached to a prothallus. The glandular hairs shrivel early and their enlarged bases are conspicuous on the margin of the cotyledon, which has only one vein.

Figure 87 indicates the root cap of the primary root and Figure 89 the tip of a young cotyledon with glandular hairs.

VII. VEGETATIVE REPRODUCTION

Regeneration was common on gametophytes of *G. billardieri* at all stages.

Figure 17 shows a young prothallus with an injured cell and a branch filament arising from the second prothallial cell. Small pieces of the filamentous prothallus showing necrosis sent out new filaments, as occurred in the filamentous gametophyte of *Polyphlebium venosum* (R.Br.) Copel. (Stone 1958).

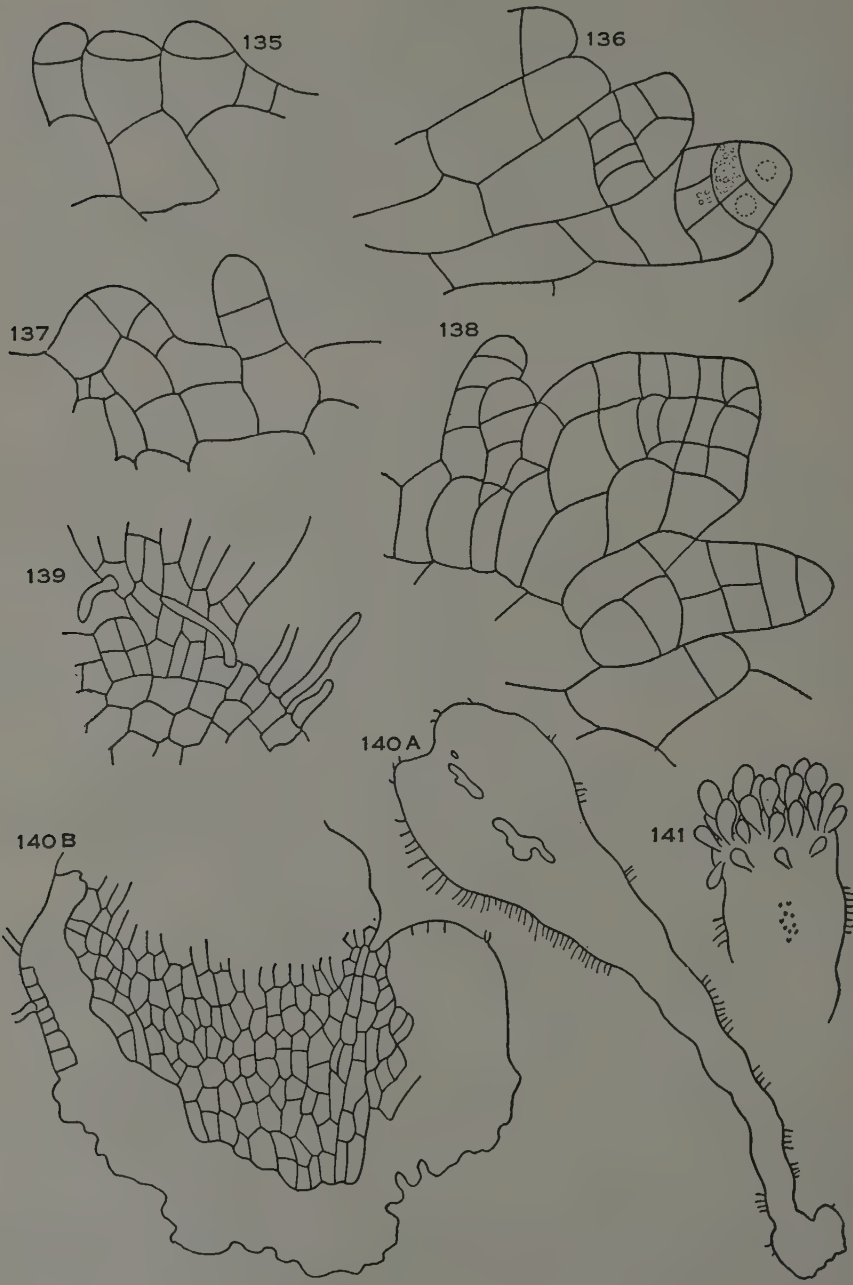
Figure 79*A* is of an immature prothallus found in the field. It showed no necrosis but the apical region had extended, probably after a period of arrested growth, to form a second prothallus. Figure 82 is a mature prothallus showing the same feature.

Mature prothalli which have partly decayed may also extend from the region of the notch and form another mature prothallus, as seen in Figure 140*A*. This new prothallus was 1 cm long and 0·8 mm wide. Figure 140*B* is the area of regeneration enlarged.

Figure 84 shows part of an old prothallus bearing four branches, each over 1 cm long, three of which bear sex organs on separated cushions. A well-developed sporophyte is present on the youngest cushion of one branch; and the fourth branch, which bears no sex organs and few rhizoids, has two small areas of regeneration near some necrosed cells.

Vegetative reproduction occurred abundantly on prothalli from which the distal part bearing young archegonia had been cut for sectioning (Fig. 141), and was also common on mature prothalli which had not been injured and which showed no browning of cells. Groups of cells or single cells became meristematic, and proliferations arose from marginal and surface cells, either dorsal or ventral (Figs. 135–139). These frequently began as filaments; the first longitudinal division occurred in a cell back from the terminal cell, and an apical cell was formed later as in the development of plates from original filaments (Figs. 135–138). They broadened comparatively quickly and developed into numerous overlapping spatulate outgrowths. No sex organs were seen on these adventitious growths.

Goebel (1888) mentioned that adventive shoots formed on the edges of prothalli of *Ctenopteris obliquata*.



Figs. 135–141.—Regeneration in *G. billardieri*. Figs. 135–138.—Regenerations from margins and surfaces of undamaged prothalli. ×210. Fig. 139.—Similar, with rhizoids. ×75. Fig. 140*A*, *B*.—*A* shows a new prothallus growing from the apex of an old necrosed prothallus. ×*c*. 8. *B*, area of regeneration enlarged. ×49. Fig. 141.—Proliferations from cut prothallus. ×*c*. 8.

VIII. ENDOPHYTIC FUNGUS

Mature prothalli of *G. billardieri* and *C. heterophylla* found growing in the field always showed the presence of coils of fungal hyphae in the parent cells of rhizoids. Gametophytes of *G. billardieri* grown to maturity on the natural substratum in the laboratory frequently showed the same condition. Sections of prothalli showed that the fungus travels up the interior of the rhizoid, and penetrates the wall to enter the rhizoidal cell to which the coils are confined (Plate 1, Fig. 2). The nucleus appeared unaffected by the presence of the fungus.

Members of the *Hymenophyllum* group of the Hymenophyllaceae investigated by the author show similar fungal coils in the rhizoidal cells when prothalli are grown on their natural substratum.

Goebel (1888) reported a similar condition existing in the prothalli of *C. obliquata*. He considered that the fungus caused the nucleus to shrink and that the irregular branching of some rhizoids could perhaps be attributed to the action of the fungus, that the fungus was a parasite and played no part in nutrition, and that the prothallus as a whole did not suffer from the infection because the rhizoids were only organs of attachment.

The rhizoids of *G. billardieri* and *C. heterophylla* branch on young prothalli in sterile cultures, so that branching rhizoids have no connection with fungal infection.

IX. DISCUSSION

The prothalli of *G. billardieri* and *C. heterophylla* are essentially alike and the typical germination is of an unusual type. The first wall divides the spore into two equal prothallial cells, and rhizoid development is delayed. The spores of *C. heterophylla*, however, show much greater variability in size, and germination is not as uniform as in *G. billardieri*. The gametophytes of both have a prolonged filamentous stage, but growth is not quite as slow in *C. heterophylla* and plate formation sets in much earlier than in *G. billardieri*. No hairs were seen on the few mature gametophytes of *C. heterophylla* which were examined.

Prothalli of *G. billardieri* also show a close resemblance to those of *C. obliquata* as described by Goebel (1888), except that rhizoids were not seen on the cushions in *G. billardieri*. Goebel gave no description of germination stages, origin of hairs, archegonia, or antheridia.

The gametophytes of these ferns of the *Grammitis* group differ from those of any other ferns which have been described in the literature, and their distinctive features show a closer resemblance to some of the more primitive rather than to the higher leptosporangiate ferns.

There is difficulty in assessing the phylogenetic value of characters of epiphytic prothalli which show specialized features, but the hairs of *G. billardieri* originate in a similar manner to those of some of the lower leptosporangiate families. The archegonial neck is longer and the antheridia slightly more complex than is customary in the higher ferns, and there is occasionally a division between the neck canal nuclei of the archegonia, a feature usually regarded as primitive. The formation of antheridia after archegonial development has proceeded for some time, and the restriction of antheridia to the cushion region is unusual, though antheridia continue to develop after archegonia begin to form in some of the more primitive leptosporangiate ferns. Rhizoids have a few chloroplasts when first formed, and the slow growth and long life of the prothallus are features usually associated with primitive ferns.

The unicellular spine-like marginal hairs of *G. billardieri* are distinct from those described for any other family. The mode of origin of prothallial hairs from a special initial cell is known to occur in the three families Gleicheniaceae, Cyatheaceae, and Loxsomaceae. The position and form of the hair in *G. billardieri*, however, are different. The hairs of the Cyatheaceae and Loxsomaceae occur on the surface instead of on the margin, and are green, multicellular, and often multiseriate with a tapered cell at the tip (Stokey 1930; Stokey and Atkinson 1956).

Prothalli of the Gleicheniaceae have hairs composed of a few cells capped with a glandular cell, and although generally superficial they are occasionally marginal and arise from a wedge-shaped initial (Stokey 1950). They are very similar to those found on an unusual *G. billardieri* prothallus.

Kachroo (1955) describes an "acicular" hair associated with club-like hairs with a glandular tip on prothalli of *Leucostegia immersa* (Wall) Presl. His figures do not indicate that they arise from a special initial, but as described for other higher ferns.

Stokey (1951) considers that any prothallus with a wedge-shaped hair initial would have a strong claim to affiliation with the Cyatheaceae or Gleicheniaceae. Holttum (1947) tentatively suggests that the Grammitidaceae may have originated from the Gleicheniaceae.

The grammitid prothalli investigated show a remarkable similarity in vegetative characters to the prothalli of the *Hymenophyllum* group of the Hymenophyllaceae. This was noted briefly by Copeland and Giauque (1950), who say that the gametophytes of the two families are similar in many respects.

In each case the trilete green spores show a strong tendency to germinate in the sporangium; however, in the *Hymenophyllum* group the spore is divided first into two, then into three cells in a triradiate manner, while in *G. billardieri* and *C. heterophylla* two approximately equal cells are formed.

The prothalli of both groups have a prolonged filamentous stage, are very slow in reaching maturity, when they are elongated and ribbon-like, and show a strong tendency to regeneration. The prothalli of the *Grammitis* group do not branch as much as do those of the *Hymenophyllum* group but they have the same dark green colour, thick cuticle, and pitted lateral walls. The rhizoids develop late, turn brown quickly, and show the same type of branching. They arise mainly on the margins, and when the prothalli are grown in the natural state show fungal coils in the rhizoidal cells. The cushions are thin, usually only two cells thick, but in the *Grammitis* group form discontinuous axial cushions, whereas in the *Hymenophyllum* group they are marginal and rarely found in the central region.

Before the cushions have developed it would be difficult to distinguish between prothalli of the *Grammitis* and *Hymenophyllum* groups unless the primary cells are still attached, but at maturity they are easily separated by the positions of the cushions, and in the case of *G. billardieri* by the very characteristic hairs, the Hymenophyllaceae always having naked prothalli. The archegonia are different, those of *G. billardieri* having a shorter recurved neck whereas those of the *Hymenophyllum* group are straight; and the antheridia of *G. billardieri* are less complex and contain fewer sperms than those of the *Hymenophyllum* group.

The likenesses in vegetative features possibly arise from the fact that these epiphytic ferns are highly specialized and adapted to a moist and shady environment, the long-living elongated prothalli being able to compete with the thick layer of mosses and lichens which grow with them. It is interesting that the sporophytes of the Hymenophyllaceae and the Grammitidaceae are adapted to similar conditions, the former by extreme thinness of the fronds, the latter by thick fronds with mesophyll cells with large intercellular spaces, while the much more simply organized gametophytes of each family have very similar vegetative features.

The prothalli of *G. billardieri* and *C. heterophylla* are unlike those of higher ferns described in the literature. Three members of the Polypodiaceae in its restricted sense have been grown by the author: *Platycerium bifurcatum* (Cav.) C. Chr., *Pyrrosia rupestris* (R.Br.) Ching (formerly *Cyclophorus serpens* C.Chr.), and *Phymatodes diversifolium* (Willd.) Pich.-Ser. (formerly *Polypodium diversifolium* (Willd.). These are all epiphytic, but have bilateral spores without chlorophyll, which germinate in the normal manner for higher ferns.

The gametophytes of *Platycerium bifurcatum* and *Pyrrosia rupestris* have short filaments and mature quickly to small cordate prothalli, bearing unicellular glandular hairs and some of a multicellular, branching type. These hairs do not arise from a special initial like those of *G. billardieri*, but as projections from the centre of marginal or superficial cells of the thallus, as found in other higher leptosporangiate ferns. The cushions are of the normal type, and the rhizoids on the ventral surface in the posterior region. Stokey and Atkinson (1954*a*) described five species of *Platycerium*, all with essentially the same type of prothallus.

The gametophyte of *Phymatodes diversifolium* also differs from those of *G. billardieri* and *C. heterophylla*. These ferns grow in similar situations except that *P. diversifolium* and *C. heterophylla* are higher epiphytes than *G. billardieri*. The filamentous stage of *P. diversifolium* is short, but the prothallus develops much more slowly than those of *P. bifurcatum* and *P. rupestris* though not nearly as slowly as those of the grammitid ferns investigated. The mature gametophyte is slightly elongate cordate, with rhizoids on the ventral surface but also often on the margins. Hairs on these prothalli are fewer, but arise in the same manner and are of the same type as those of other Polypodiaceae.

The antheridia of *G. billardieri* are slightly more complex, and also differ in origin, position, and order of appearance from those of the Polypodiaceae, where they arise as a protrusion from the surface of a cell, are normally produced before the appearance of archegonia, and typically have three wall cells—the stalk, ring, and cap cells. Antheridia of the Polypodiaceae also show fewer sperm cells than those of *G. billardieri*.

The prothalli of *G. billardieri* and *C. heterophylla* show some similarity in their specialized features to those of species of *Elaphoglossum* Schott and *Rhipidopteris* Schott described by Stokey and Atkinson (1957). These epiphytic ferns have an elongated thallus with marginal rhizoids and thin cushions which are sometimes discontinuous, but they do not possess the primitive tendencies shown by *G. billardieri*. The antheridia are simpler, and the hairs produced by *Elaphoglossum* arise as in the higher ferns.

The embryo of *G. billardieri* shows a development of enlarged haustorial type cells in the foot similar to those figured by Stokey and Atkinson (1957) for *Elaphoglossum tectum* Bell, and by Ward (1954*b*) for *Phlebodium aureum*.

The study of the gametophytes of *G. billardieri* and *C. heterophylla* leads to the conclusion that the separation of the family Grammitidaceae from the Polypodiaceae on sporophytic characters is supported by the gametophytic generation. The prothallus of *G. billardieri* has specialized features which show no close relationship to the characters of the advanced ferns so far described.

X. Acknowledgments

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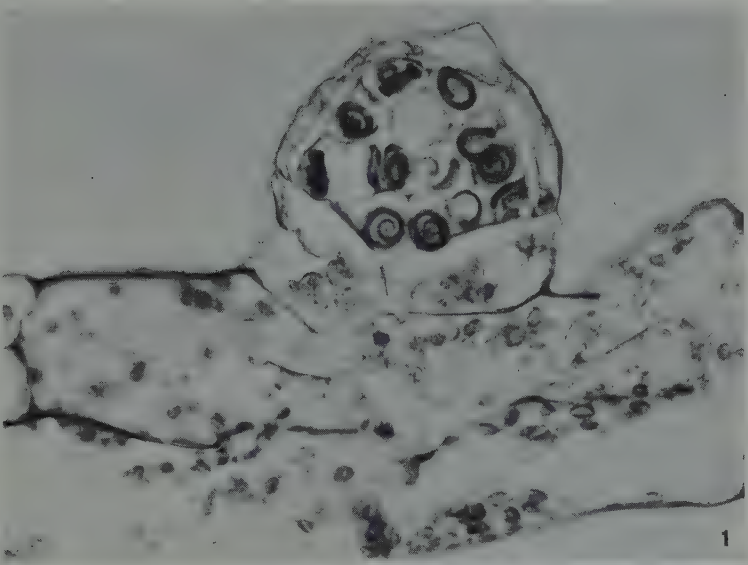
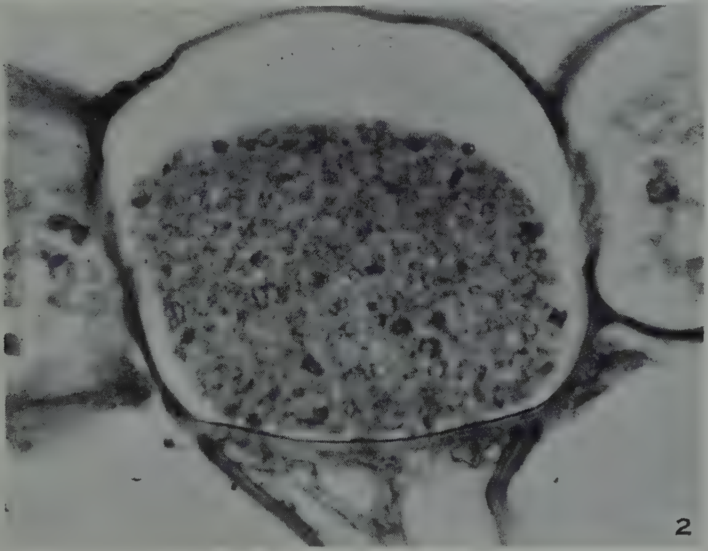
GAMETOPHYTES OF G. BILLARDIERI AND C. HETEROPHYLLA





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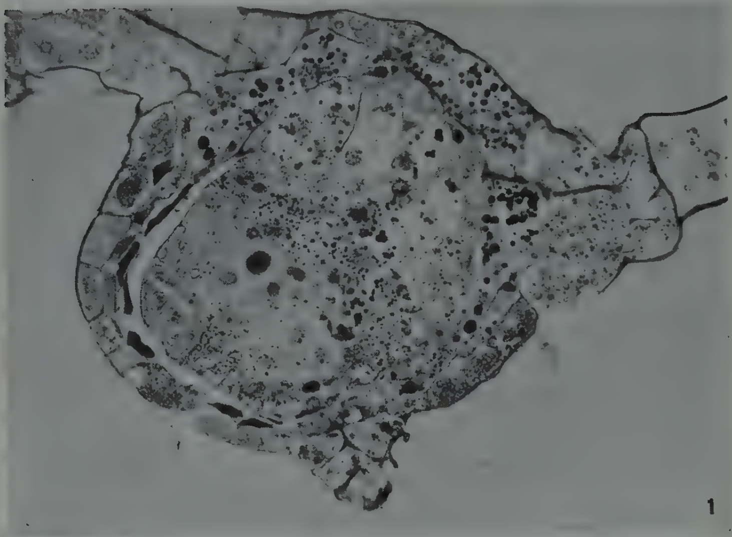

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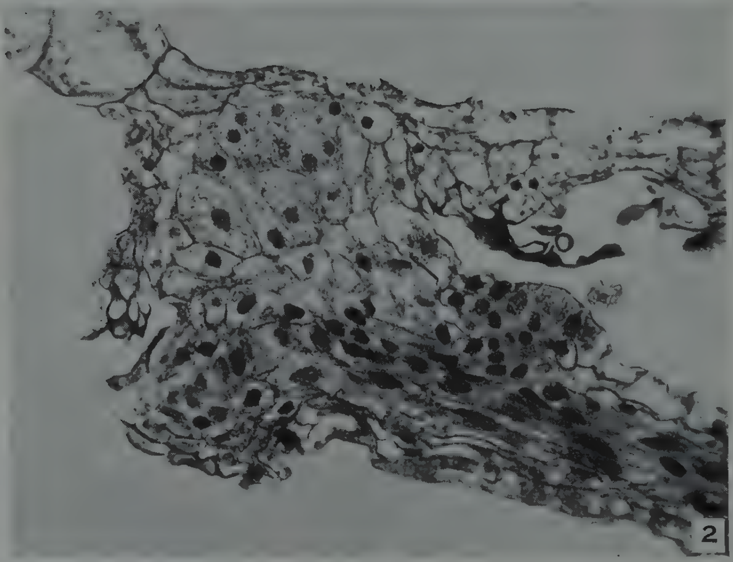

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ADDENDUM

Since the completion of this work, an article by Stokey and Atkinson has appeared in *Phytomorphology* (8: 391–403 (1958)) entitled "The gametophytes of the Grammitidaceae". The distinctive features of the gametophyte of *Grammitis billardieri* differ in some major respects from those members of the *Grammitis* group dealt with by these authors.

EXPLANATION OF PLATES 1 AND 2

PLATE 1

G. billardieri

Fig. 1.—Longitudinal section (not median) of an antheridium, showing two nuclei, and dividing wall in the basal cell. Ventral surface up. ×730.

Fig. 2.—Section showing endophytic fungus in rhizoid and parent cell. ×1200.

PLATE 2

Sagittal sections of embryos of *G. billardieri*, dorsal surface up. ×250.

Fig. 1.—Embryo enclosed in calyptra. Note very large cells of foot penetrating the jacket cells; root region near remains of archegonial neck; prominent apical cell of cotyledon; stem region opposite the root; pitted lateral walls of prothallus at left of embryo.

Fig. 2.—Embryo which has burst from the calyptra. Rudimentary vascular tissue between cotyledon, root, and stem. Note very thin cushion from which embryo projects strongly.

STUDIES OF THE FAMILY PROTEACEAE

I. ANATOMY AND MORPHOLOGY OF THE ROOTS OF SOME VICTORIAN SPECIES

By Helen M. Purnell*

[*Manuscript received October* 15, 1959]

Summary

The term "proteoid root" is defined. The morphological and anatomical features of such roots are described. A short account is given of the anatomy of the primary root and of roots in which secondary growth has occurred. The types of root system found among representative Victorian genera are also described.

I. Introduction

Along the lateral roots of many members of the family Proteaceae arise dense clusters of rootlets of limited growth. It is proposed to refer to each cluster of rootlets as a "proteoid root" and to that section of the lateral root from which the rootlets arise as the "axis of the proteoid root". The general appearance of "proteoid roots" can be seen in Plate 1, Figures 1–4.

No detailed studies of the general root structure or of the unusual "proteoid roots" appear to have been published. Engler (1889) commented on the thick "absorption hairs" on the ultimate roots of species cultivated in botanical gardens, and Broadhurst (1954) described the development of "anomalous roots" on *Hakea pugioniformis*,† but neither author gave details of their structure. In this paper the root morphology and anatomy of representative species of the genera of Proteaceae occurring in Victoria are described. Reference is also made to a few of the commonly cultivated species.

II. Materials and Methods

The roots used in these studies were collected in the field, either from seedlings or from shrubs small enough to be dug out. Fresh material was hand-sectioned. Microtome sections were prepared from material fixed in formalin-acetic-alcohol and embedded in paraffin wax. Observations were made on the external features of the root systems of many species, and a few were examined in detail. The structure of the primary root was worked out from material collected from plants growing in pots or from seeds germinated in a moist chamber.

III. Morphology of the Root Systems

At the seedling stage there is, in all species, a short tap-root with numerous laterals. Later the roots of different species develop in different ways, and several types of mature root systems may be distinguished as follows:

(*a*) The tap-root remains prominent and few large lateral roots are developed.

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†Authorities for specific names appearing in this paper are given in Appendix I.

(*b*) The tap-root either fails to develop after the seedling stage, or it develops and later decays and a system of long thick lateral roots is produced close to the surface of the soil.

(*c*) Similar to the previous type, but with the addition that sucker shoots develop on the branching, subsurface lateral roots.

Species such as *Adenanthos terminalis*, *Banksia serrata*, *Conospermum mitchellii*, *Grevillea lanigera*, *Isopogon ceratophyllus*, *Lomatia ilicifolia*, and *Telopea oreades* are among those which conform to type (*a*). This type of root system was described by Specht and Rayson (1957) for *Adenanthos terminalis* and other heath plants. The tap-roots of *Conospermum mitchellii* and *Lomatia ilicifolia* typically develop into thick, distorted, woody structures from which numerous aerial shoots and small lateral roots arise.

The root systems of *Hakea sericea*, *H. ulicina*, and *Grevillea chrysophaea* generally conform to type (*b*). On sandy heathland soils the subsurface roots of *H. ulicina* and *H. sericea* have been found to grow up to 15 ft long. These species sometimes have a fairly well-developed tap-root in addition to the extensive lateral root system.

Grevillea parviflora and *Banksia marginata* are species which conform to type (*c*). Specht and Rayson (1957) have described this type of root system for *B. marginata* growing on the heathlands of the Ninety-Mile Plain.

Specht and Rayson (1957) have pointed out that heath species which have a deep tap-root or a horizontal suckering root system with buds below the soil surface are able to regenerate readily after fire. *Lomatia ilicifolia*, which is widespread in sclerophyllous forest country and on heathlands, is one of the first shrubs to regenerate after a fire, and on each plant up to eight root suckers appear and grow rapidly. Similarly after a heathland fire, root suckers from the thickened tap-roots of *Conospermum mitchellii* and *Isopogon ceratophyllus* and from the horizontal subsurface root system of *Banksia marginata* are among the first green shoots to appear. It will be shown that the root systems of these species contain reserves of starch which would provide a food supply for such a period of rapid growth. On the other hand, plants of species such as *Hakea ulicina*, *H. sericea*, and *Grevillea chrysophaea* are readily killed by fire, and all regeneration must come from seedling growth.

IV. Anatomy of the Primary Root

The general arrangement of the tissues in the primary roots of the species examined is illustrated in Plate 4, Figure 1.

(*a*) *The Meristem*

Because of the necessity of examining exactly median longitudinal sections cut with a microtome, this study of the structure of the apical meristem is restricted to two species of *Hakea*, *H. eriantha* and *H. sericea*, and two species of *Banksia*, *B. collina* and *B. marginata*.

On examination of median longitudinal sections through the meristem, several cell complexes may be distinguished (Plate 5, Fig. 1). These are arranged to form the same kind of pattern as those of the roots of *Fagus sylvatica* L., described by Clowes (1950). A broad columella forms the central section of the root cap. The promeristem, as in *Fagus*, consists of a large group of cells arranged in the form of an inverted cup, resting on a saucer. The columella is continued through the cup and terminates in a group of meristematic cells forming the bottom of the cup. On the proximal side of the apical cup these meristematic cells give rise to the plerome. The initials of the peripheral part of the root cap and the periblem form the sides of the cup (Fig. 1).

The majority of cell divisions in the columella occur in the transverse plane, so that the number of rows of cells remains constant. Cells are added to these rows by the division of a layer of meristematic cells, forming the saucer. Cells of the columella distal to the promeristem are highly vacuolate and enlarged. In the longitudinal median plane, there appear to be about six plerome initials and these are most irregular in shape. The central portion of the plerome is composed of cells which divide almost exclusively in the transverse plane. In the outer section of the plerome, numerous periclinal divisions occur and these show a T pattern (Wagner 1939), with the capital of the T directed towards the initials.

The periblem initials lie at the sides of the cup-shaped promeristem, between the plerome initials and those of the peripheral part of the root cap (Fig. 1). As in the outer section of the plerome, the periclinal T divisions occur with the capital of the T directed towards the promeristem. The piliferous layer and the peripheral part of the root cap originate from the same cell complex. By numerous periclinal T divisions, with the capital of the T directed away from the initials, the piliferous layer differentiates from the peripheral part of the root cap. The rows of cells can be traced towards the apex as far as the columella, and the root cap typically tapers to quite a sharp point.

Cell elongation and vacuolation first commence, and subsequently proceed most rapidly, in the cells of the central section of the plerome. These cells finally differentiate into the xylem elements. Vacuolation in the plerome is soon followed by vacuolation of cells in the central section of the cortex. About the same time, deposition of material resembling tannin commences in two layers of cells, the inner of which finally constitutes the endodermis. Tannin deposition commences earlier in this inner layer.

The cells of the piliferous layer are characteristically regular in size, shape, and depth of staining. This feature provides confirmation for the observation that every cell of the piliferous layer may ultimately develop a root hair.

(*b*) *The Root Cap*

The structure of the root cap in *Lomatia longifolia*, *Grevillea chrysophaea*, *Isopogon ceratophyllus*, and *Persoonia juniperina* follows the pattern already described for *Hakea sericea* (Plate 5, Fig. 1). Oliphant (1956) commented on the prominent dark-coloured root caps on the main and lateral roots of *Banksia marginata*. The root caps of *Banksia collina*, *B. integrifolia*, and *B. serrata* are similar to those of *B. marginata*. The dark colour of the root caps is due to the deposition of tannin mainly in the peripheral cells (Plate 5, Fig. 2). The older cells of the root caps of the

Banksia spp. are very much more persistent than those of the *Hakea* type and form a kind of veil around the root (Plate 9, Fig. 3).

(*c*) *The Piliferous Layer*

The cells of this layer are of approximately equal size. The root hairs emerge from the part of the cell nearest to the root apex. In roots of small diameter each of the epidermal cells appears to form a root hair but in larger roots small, scattered strips of cells may be free of them. These cells do not outwardly appear to differ from the piliferous cells. The root hairs vary in size from species to species, but the most usual range is about 200–400 μ in length and 7–10 μ in diameter. The root hairs developed on the primary root when seeds were germinated in a moist chamber

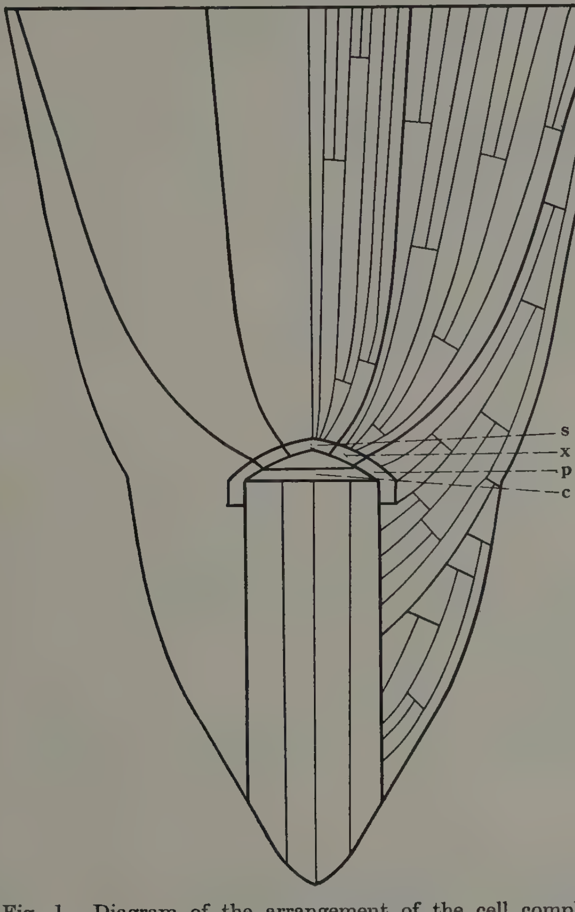

Fig. 1.—Diagram of the arrangement of the cell complexes and the pattern of periclinal cell divisions seen in a longitudinal section of the primary root of *Hakea sericea*. The meristematic cells giving rise to the cell complexes are designated as follows: *c*, columella; *p*, peripheral section of the root cap and the epidermis (*e*); *s*, stele; *x*, cortex.

were up to 2 mm long. Short root hairs are sometimes found scattered among the long ones, a condition which Cormack (1949) has suggested may be due to suppression of the development of some of the hairs rather than to the emergence of new hairs between the older ones. In the Proteaceae the root hairs are usually distorted towards their tips and occasionally they fork or produce small branches (Plate 9, Figs. 4, 5). The root hairs are typically persistent, and have been observed on epidermis that had commenced to slough off after the root had undergone considerable secondary growth. Persistent root hairs on species belonging to many other families have been reported by Dittmer (1949).

(*d*) *The Cortex*

The cortex consists of 6–15 rows of more or less radially arranged cells. The majority of the cells appear to be normal parenchyma and there are occasionally a few scattered cells with granular contents. There are always intercellular spaces between the cortical cells. In some species the cell walls are relatively thick, with simple pits between the cells. Thickening in the inner cortex occurs at an early stage, for thick-walled pitted cells are seen before the differentiation of the first metaxylem element. The cells of the innermost one or two layers and of the subepidermal layer are frequently only about half the size of the remaining cortical cells.

(*e*) *The Endodermis*

In the species examined the cells of the endodermis appear to be quite normal in structure, and the Casparian strips are confined to radial walls. As mentioned above, deposition of tannin in the cells of the endodermis commences close to the meristematic region. Initially, the tannin is confined to cells on the same radii as the protophloem poles, and then deposition spreads to the remainder of the endodermis. Clowes (1951) noted a similar pattern of tannin deposition in the endodermis of the roots of *Fagus sylvatica*. At the same time tannin forms in the majority of the cells in the innermost layer of the cortex. Thickening of the endodermal cell walls occurs first in the region of the protophloem poles, and two or three cells opposite the protoxylem poles remain unthickened for a short period.

(*f*) *The Pericycle*

The pericycle is uniseriate and composed of thin-walled parenchyma cells. Many of the cells adjacent to the phloem poles become impregnated with tannin, and tannin may also occur in cells at the sides of the phloem bundles (Plate 4, Fig. 1). Some of the cells of the pericycle, usually those between the xylem and phloem poles, divide periclinally even before the metaxylem is fully differentiated.

(*g*) *The Vascular System*

The number of protoxylem poles varies from four to seven. The number is not constant for a given species. *Hakea sericea*, for instance, has been observed to have either tetrarch or hexarch roots. The xylem elements are tracheids and pitted or spirally thickened vessels. The metaxylem finally occupies the entire centre of the stele. The sieve elements of the phloem are small in diameter and have slightly oblique sieve plates in the end walls. There is only one companion cell to each sieve element. Some thin-walled parenchyma is also present but no fibres are differentiated. The primary structure of the normal root presents no morphological peculiarities and is fairly uniform throughout the family.

V. General Anatomy of the Secondary Root

Secondary growth of the vascular tissue is initiated by cell divisions which occur on the inner margins of the phloem strands, and strips of cambium form in these positions. These isolated strips of cambium cut off, to the inside, rows of cells which give rise to a considerable number of secondary xylem elements, so that the sectors between the protoxylem poles are finally filled in with xylem. Then the cambium becomes continuous as the pericyclic cells to the outside of the protoxylem poles become meristematic. In Plate 3, Figure 2, and Plate 4, Figure 3, stages in early secondary growth are illustrated. Esau (1943) described a similar sequence of development in the root of pear (*Pyrus communis* L.).

The secondary vascular tissue is traversed by rays which are either uniseriate or multiseriate and in which both upright and procumbent cells occur. The rays vary considerably in height, ranging from 1 or 2 cells to more than 200. The rays radiating from the protoxylem poles are multiseriate in all species examined except *Persoonia juniperina*, in which most of the rays are uniseriate. In species with both multiseriate and uniseriate rays, the uniseriate rays rarely originate in the primary tissue, and if they do, they radiate from between the protoxylem poles. These observations agree with those made by Barghoorn (1940) for the roots of woody dicotyledons in general. Secondary rays, that is, those which as the root increases in girth, originate from new ray initials cut off from fusiform initials, are commonly uniseriate at first and may become multiseriate after a further period of growth. The thick tap-roots of *Isopogon ceratophyllus* and *Lomatia ilicifolia* have extremely wide multiseriate rays which make up about two-thirds of the secondary wood (Plate 7, Fig. 1). These rays are also very high and frequently divide, presumably by the transformation of ray initials into fusiform initials. The large multiseriate rays of *Conospermum mitchellii*, *Adenanthos terminalis*, and some *Banksia*, *Hakea*, and *Grevillea* spp. also divide in this way (Plate 7, Fig. 3).

In the thick lateral roots of *Hakea sericea* and *Grevillea lanigera* the cells of the multiseriate rays are of various shapes. In transverse section the cells in the centre of the ray are more or less rectangular, those on either side are longer with slightly oblique end walls, and sometimes the flanking cells are long and narrow with very oblique end walls (Plate 8, Fig. 4). In specimens of *Hakea sericea* and *Grevillea lanigera* with wide rays, the cambium giving rise to the ray tissue curves sharply towards the centre of the root (Plate 8, Fig. 2). This curve is not reflected on the surface of the root and it is evident that the number of ray cells formed on the phloem side increases with the depth of the curve.

In all species the ray cells are parenchymatous, with moderately thick walls in which there are simple pits. The majority of the cells are packed with starch grains, and cells with tanniferous contents are also common.

Examination of transverse sections of secondary roots shows considerable variation in the arrangement of the vessels and other xylem elements. In *Isopogon ceratophyllus* the pores are predominantly solitary and there may be a few tangential pairs (Plate 7, Fig. 1). In *Conospermum mitchellii* and *Persoonia juniperina* they are solitary or arranged in tangential multiples of two to six. In *Hakea sericea* large and small vessels are grouped into distinct bands (Plate 7, Fig. 2). The end walls of the vessels are more or less oblique, and simple perforation plates are found in all the species examined. Reticulate perforation plates also occur in some of the vessels of *Telopea oreades* and *Lomatia ilicifolia* (Plate 6, Fig. 2). In most species the bordered pits of the vessels are small and alternately arranged. In *Banksia* spp. some of the vessels have scalariform bordered pits (Plate 6, Fig. 1). Spiral thickenings have been observed on the walls of some of the vessels in *Persoonia juniperina*, *Banksia collina*, *Grevillea aquifolium*, *G. parviflora*, and *Hakea ulicina*. The xylem of the majority of species contains many true tracheids with long, tapering end walls, bordered pits, and in some cases spiral thickenings. In *Hakea* and *Grevillea* spp. particularly, fibre tracheids and fibres make up the ground tissue between the vessels. In other species, such as *Banksia serrata* and *B. collina*, many of the vessels are very small and difficult to distinguish from the tracheids and fibres of the ground tissue.

Xylem parenchyma is abundant in most of the species examined. In the majority of cases it is paratracheal and occurs on the abaxial side of the vessels with which it is associated (Plate 7, Fig. 4). Vasicentric parenchyma is occasionally seen in *Isopogon ceratophyllus* and *Lomatia ilicifolia*. The xylem parenchyma cells are normally long with tapering end walls. They are usually rich in starch grains and may have tanniferous contents. The general characteristics of the secondary xylem of the roots are in agreement with those described by Chattaway (1948) for the secondary wood of the Proteaceae.

The phloem rays are continuous with the multiseriate and uniseriate rays of the xylem. In general, the cells of the phloem rays contain little starch but may contain tannin. In many species, sclereids occur in the outer sections of the phloem rays and occasionally they form quite close to the cambium. The part of the phloem next to the cambium consists of functional sieve tubes and companion cells and phloem parenchyma (Plate 6, Fig. 4). The end walls of the sieve elements are oblique and occupied by large compound sieve plates (Plate 6, Fig. 3). Sieve areas also occur along a large proportion of the lateral walls of the sieve elements. The companion cells are very narrow and as long as the sieve elements. The phloem parenchyma cells resemble the sieve elements in shape and size and have some starch stored in them. As new phloem tissue is produced by the cambium during a new growth period, the tissue formed in the previous period undergoes considerable changes. The companion cells disappear and the sieve tube walls are partly crushed. It is at this stage that the phloem is presumed to have lost its conducting function (Esau 1943). Eventually the sieve tubes are visible only as crushed wall material between the expanding phloem parenchyma cells and the differentiating sclerenchyma fibres (Plate 8, Fig. 1). The cells of the phloem parenchyma at this stage of development are isodiametric, as the original elongated cells have divided by transverse and radial walls. In the majority of species, the sclerenchyma tissue is composed solely of fibres. In the functional phloem, the cells which will give rise to the fibres are indistinguishable from cells of the phloem parenchyma, and do not differentiate as fibres until the next growing season. A similar type of fibre development has been described by Artschwager (1943) for guayule (*Parthenium argentatum* Gray) and by Schneider (1945) for cherry (*Prunus avium* L.). In *Banksia serrata* and *B. collina* some of the fibres are differentiated at the same time as the sieve elements. In the former species the precociously formed fibres are in scattered groups, while in the latter they occur in two or three radial rows on either side of the primary rays. In these species many additional fibres are eventually formed in the non-functional phloem, and a solid mass of fibres is found in the outer section of the phloem.

There is very little sclerenchyma in the outer phloem of *Conospermum mitchellii* and *Persoonia juniperina*. In these species, transverse divisions in the phloem parenchyma cells, followed by the enlargement of the derivative cells, give rise to a thick band of tissue, thus increasing the apparent width of the cortex. In longitudinal sections the origin of this "secondary cortex" is obvious. Scattered groups of elongated sclereids differentiate in the outer phloem of *Persoonia juniperina* (Plate 8, Fig. 3). On the other hand, the sclerenchyma tissue in *Isopogon ceratophyllus* is composed entirely of isodiametric sclereids which differentiate in the outer cortex and form a continuous sheath, three to five cells wide, around the root.

A cork cambium is differentiated in all species. Cork cells are cut off to the outside. To the inside a few rows of parenchyma cells, containing starch, are contributed to the cortex.

Some of the cells in the secondary cortex of *Conospermum mitchellii* proliferate, giving rise to numerous projections on the root surface (Plate 2, Fig. 2). Examination of transverse or longitudinal sections through one of these projections shows, in the centre, a group of cells with thick walls in which there are numerous simple pits (Plate 9, Fig. 1). Starch grains, which are abundant in the cells of the surrounding parenchyma, are absent from the thickened cells. The function of these cells or of the projections which contain them is a matter for conjecture.

VI. Anatomy of the Proteoid Root

The proteoid root has already been defined as the cluster of rootlets, of limited growth, which forms on a lateral root. The particular section of the lateral root which bears it is referred to as the axis of the proteoid root. The rootlets which constitute the proteoid root will be known as proteoid rootlets. In species of *Adenanthos*, *Conospermum*, *Grevillea*, *Hakea*, *Isopogon*, *Lomatia*, *Orites*, and *Telopea* examined, the axis of the proteoid root is unbranched and may be from ¼ to 1½ in. long (Plate 1, Figs. 1–3). In the Victorian species of *Banksia*, viz. *B. collina*, *B. integrifolia*, *B. marginata*, *B. ornata*, and *B. serrata*, the axis of the proteoid root is branched. The branching is profuse, particularly in older plants, so that the proteoid root may become a very complex structure. In *Banksia* seedlings the branched axis is 1–2 in. long, and in mature trees may be up to about 6 in. long (Plate 2, Fig. 1) (Oliphant 1956).

The proteoid rootlets are crowded together in longitudinal rows along the axis, and apparently most of them emerge at the same time (Plate 1, Fig. 4). In

Banksia spp. the axis branches before the emergence of the rootlets (Plate 2, Fig. 1). Young proteoid roots are covered with long root hairs (Plate 1, Fig. 2). Like those of the primary roots, the root hairs are frequently distorted or even forked at their tips. They are relatively short-lived, however, and are shed after about 3 months.

Examination of a transverse section through the axis of a simple or compound proteoid root shows that the rootlets arise endogenously opposite the protoxylem poles (Plate 3, Figs. 1, 2, and Plate 4, Fig. 3). Considerable disruption of the cortical tissue occurs as the rows of rootlets push through it. A longitudinal section through the axis shows the crowding of the rootlets in the rows (Plate 9, Fig. 2). The axis of the proteoid roots may have already undergone some secondary growth before the emergence of the rootlets. Transverse sections of roots which show this are illustrated in Plate 3, Figures 1 and 2, and Plate 4, Figure 3. It is thought that in a limited number of cases the axis may produce successive crops of rootlets, but detailed information on this phenomenon is not yet available.

The proteoid rootlets have normal primary root structure and do not undergo secondary growth. A transverse section of a proteoid rootlet (Plate 4, Fig. 2) shows that the vascular tissue is limited to two small groups of xylem and phloem. As in the primary root, the cells of the endodermis always stain deeply, apparently owing to the presence of tannin. The cortex consists of a few rows of large thin-walled parenchyma cells. Examination of a longitudinal section of a proteoid rootlet (Plate 4, Fig. 4) shows that the structure is similar to that described for the primary root. There is a small columella, the peripheral part of the root cap and the piliferous layer are derived from the same cell complex, and the cortex and stele arise from separate groups of meristematic cells. When the rootlets stop growing, root hairs may be formed right to the tip.

Proteoid roots begin to form on seedlings about the time the cotyledons are shed (Broadhurst 1954). This may occur from 2 to 6 months after germination, depending on the species and the conditions under which the plants are grown. Most of the proteoid roots form on the new lateral roots. As the proteoid rootlets break through the epidermis and grow rapidly, the lateral root continues to elongate and a succession of proteoid roots may form along its length. Broadhurst (1954) states that proteoid roots do not appear to be seasonal, and this does seem to be the case where plants are cultivated under conditions where water is not a limiting factor. In the field, however, it seems that proteoid roots are seasonal structures. Young roots are usually found only on plants dug up during winter and spring. At the end of the summer, the proteoid roots are dry and often quite shrivelled.

In order to follow the formation and development of proteoid roots, plants were grown in soil enclosed in glazed frames, as described by Ashton (1956). A frame is made of two sheets of thick glass, 18 by 24 in., set vertically ½ in. apart and held in position by a wooden framework. A piece of galvanized iron fitted to the outside of each piece of glass can be removed for inspection purposes. Two such frames were set up in January 1957, each being filled with soil from the natural habitats of the plants to be studied. Plants, which had been collected in the field and then grown on in pots for some months, were then transferred to the frames. The species studied were *Banksia marginata* and *Grevillea chrysophaea*. Since the block of soil enclosed between the two sheets of glass is very narrow, many of the roots grow down against the glass and the proteoid roots were rather flattened. The frames were inspected about every 3 months and the position of the proteoid roots marked on the glass by means of a special marking ink. From these and similar observations over a period of 2 years, it can be stated that, in general, the majority of the proteoid roots shrivel and disappear completely in about 12 months and the remainder may persist for an additional 6 months. As has been stated earlier, the root hairs only persist for about 3 months and it is presumed that the proteoid roots are functional for this period only.

VII. Distribution of Proteoid Roots in the Family Proteaceae

Species belonging to the genera *Adenanthos*, *Banksia*, *Conospermum*, *Grevillea*, *Hakea*, *Isopogon*, *Lomatia*, *Orites*, and *Telopea* have been found to form proteoid roots. A detailed list of species examined will be found in Appendix I. The only representatives of the genus *Persoonia* examined, viz. *P. linearis* Andr., *P. juniperina* Labill., and *P. pinifolia* R.Br., apparently do not form proteoid roots. The position of the other species in the genus *Persoonia* and the other Australian genera in the group Persoonieae will be the subject of further investigations.

VIII. Function of the Proteoid Root

Because of the presence of fungal hyphae in the cortical cells of many of the proteoid root axes sectioned in the early stages of this work, it was thought that the roots were an unusual type of mycorrhiza. Further observations showed that hyphae were not present in young proteoid roots, and in fact their presence in any root was unusual. It is believed, however, that initiation of proteoid roots is due to a biological stimulus, as preliminary experiments have indicated that they do not form under sterile conditions. Broadhurst (1954) stated that plants of *Hakea pugioniformis* grown in sterile flasks for 1 year failed to form proteoid roots.

There is some evidence that the proteoid roots are involved in the uptake of nutrients, particularly of phosphorus and nitrogen, by the plant. Seedlings of *Hakea laurina* were planted in a glazed frame of the type described earlier. The top 6 in. of soil in the frame was washed quartz sand. Under this was a thin layer of commercial blood and bone manure, and the rest of the frame contained sand from a heath community. There was no formation of proteoid roots in the part of the frame containing the quartz sand, but a dense layer of them formed in the section containing the blood and bone. Further experiments on the nutritional aspect will be described elsewhere.

IX. Acknowledgments

The author is indebted to Dr. and Mrs. D. J. Carr, who have given help and encouragement throughout, to Dr. Carr for help with the manuscript, and to all those who have assisted by collecting material. She is grateful to Miss Hilary Oliphant for permission to reproduce the photographs in Plate 1, Figure 3, and Plate 2, Figure 1, and to Mr. E. Matthaei and Mr. R. Oldfield, Microscopy Department, University of Melbourne, who prepared the photographs in Plates 1–5. The work was carried out in the Botany Department, University of Melbourne, and thanks are due to Professor J. S. Turner and the Forests Commission for making the facilities available.

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Explanation of Plates 1–9

Plate 1

Fig. 1.—*Telopea truncata*. Proteoid roots from which root hairs have been shed. Natural size.
Fig. 2.—*Hakea sericea*. Young proteoid root, covered with root hairs. ×6.
Fig. 3.—*Banksia marginata*. Young proteoid roots. Natural size.
Fig. 4.—*Hakea sericea*. Developing proteoid root. ×6.

Plate 2

Fig. 1.—*Banksia marginata*. Development of complex proteoid root. The axis is profusely branched, the root caps dark and prominent. ×2.
Fig. 2.—*Conospermum mitchellii*. Surface view of tap-root. ×4.

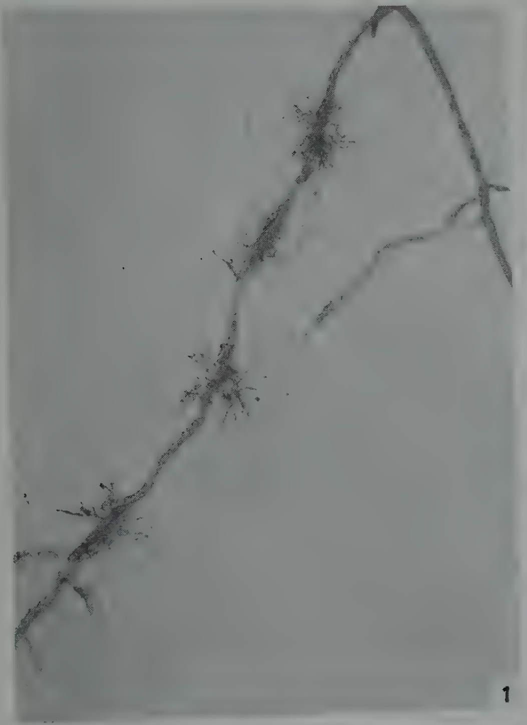
Plate 3

Fig. 1.—*Lomatia ilicifolia*. Transverse section of proteoid root axis which has undergone secondary growth. ×50.
Fig. 2.—*Hakea ulicina*. Transverse section of proteoid root axis. ×35.

Plate 4

Fig. 1.—*Hakea eriantha*. Transverse section of primary root. ×80.
Fig. 2.—*Hakea ulicina*. Transverse section of proteoid rootlet. ×200.
Fig. 3.—*Hakea ulicina*. Transverse section through axis of developing proteoid root. ×75.
Fig. 4.—*Hakea ulicina*. Longitudinal section of proteoid rootlet. ×120.

STUDIES OF THE FAMILY PROTEACEAE. I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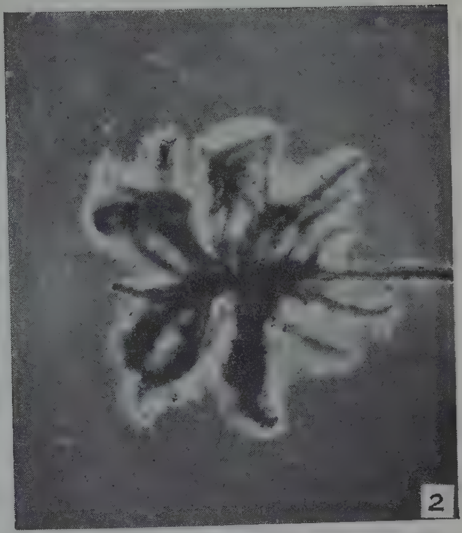
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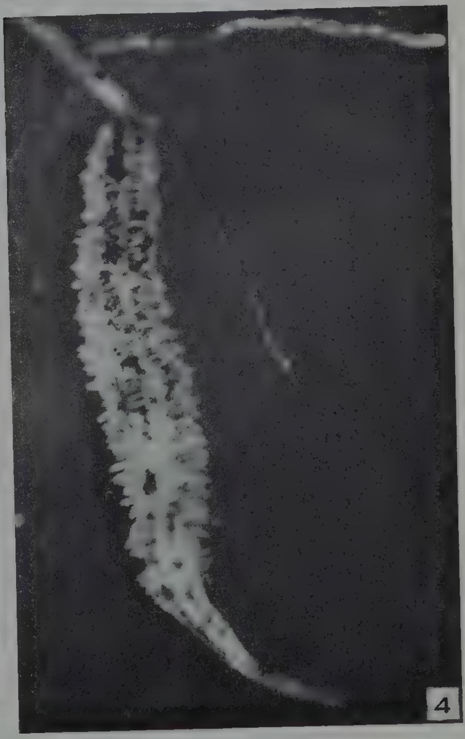
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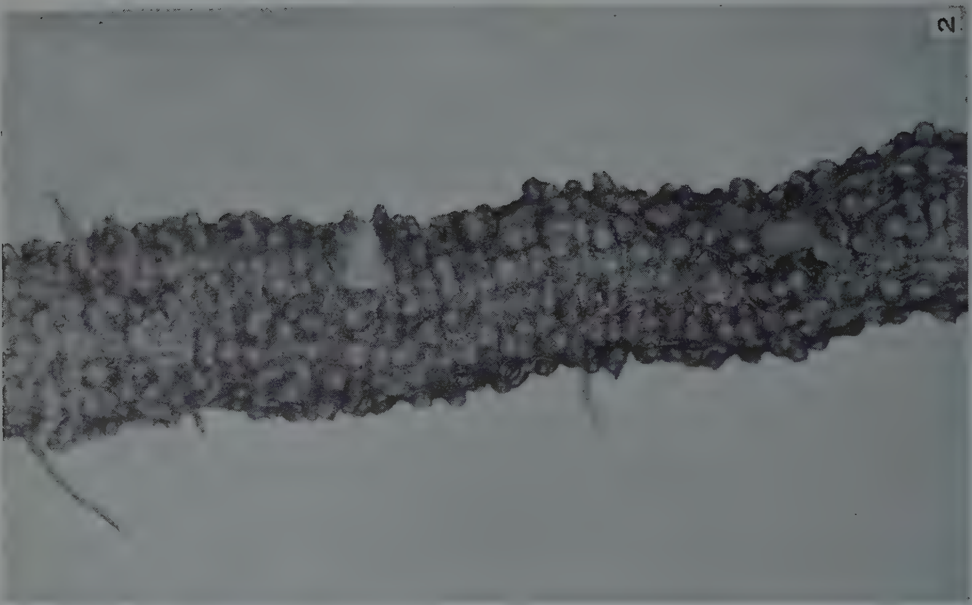

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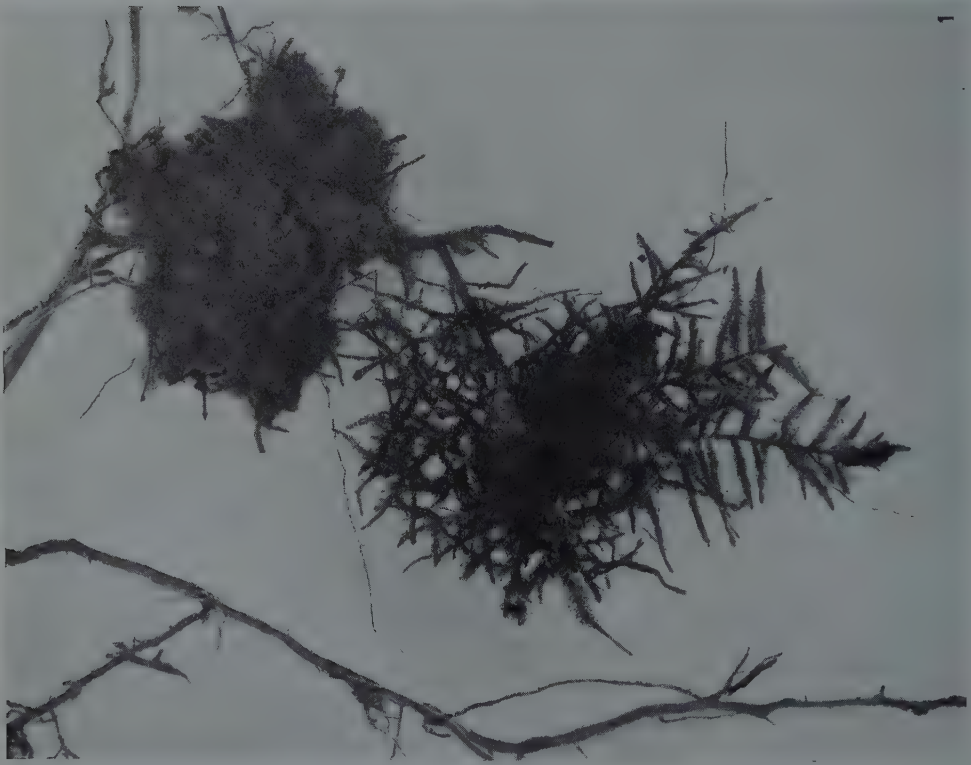

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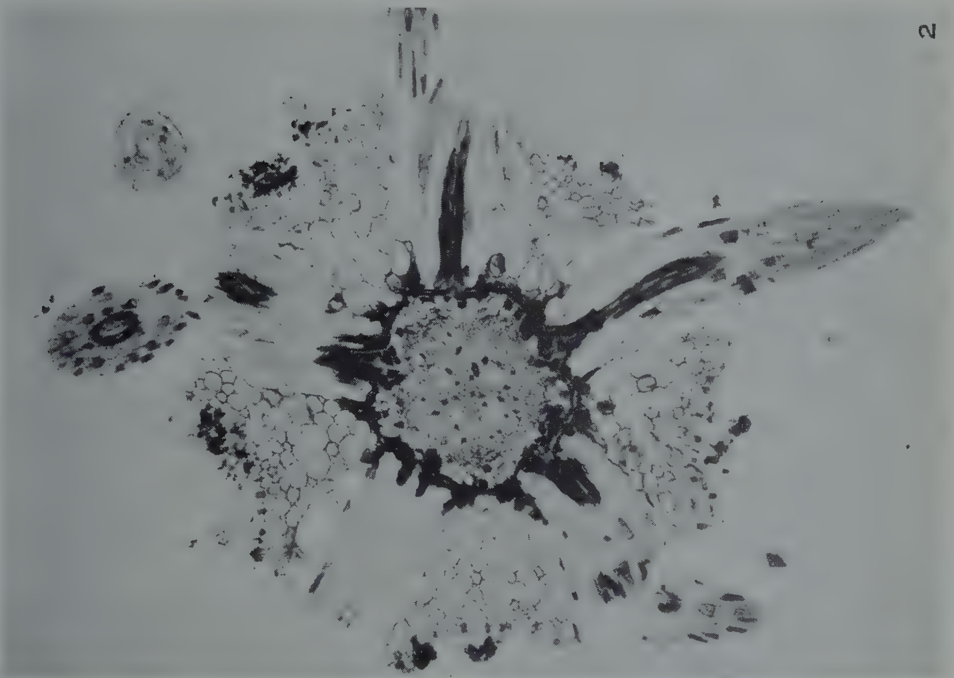

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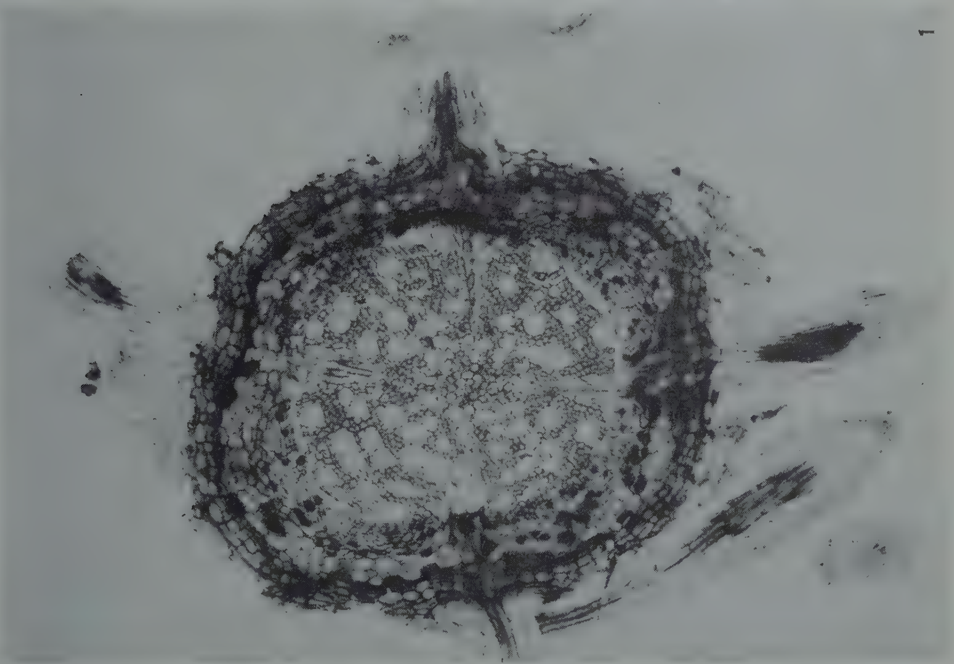

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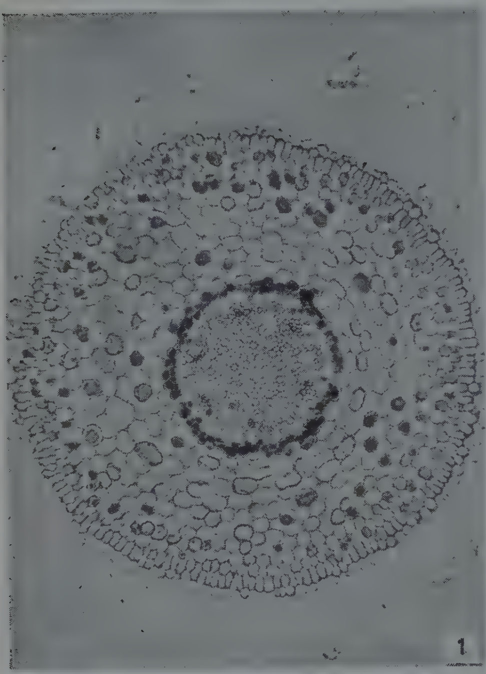

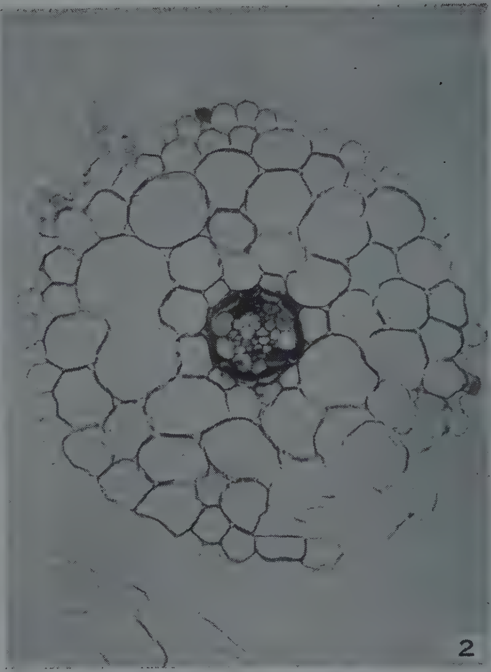

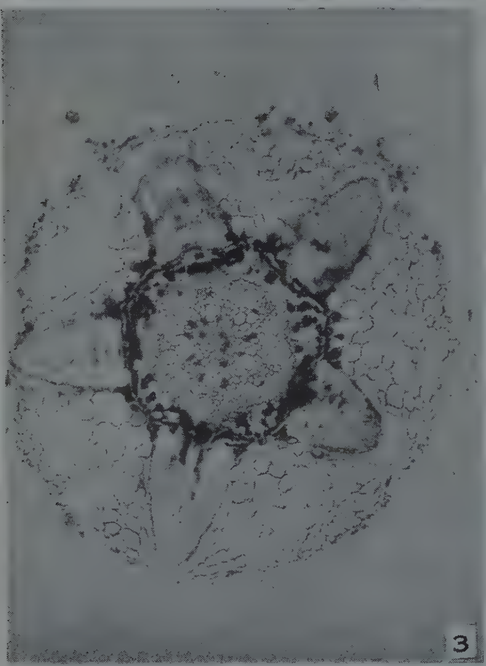

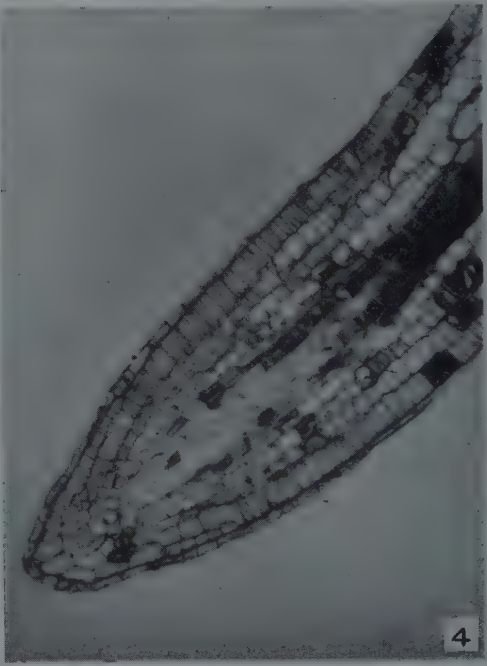

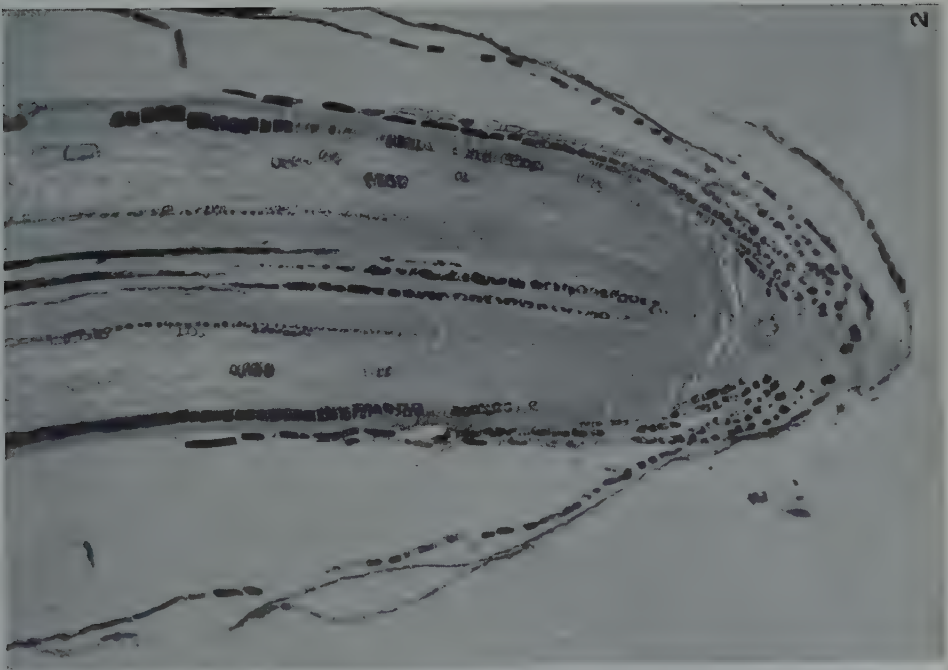
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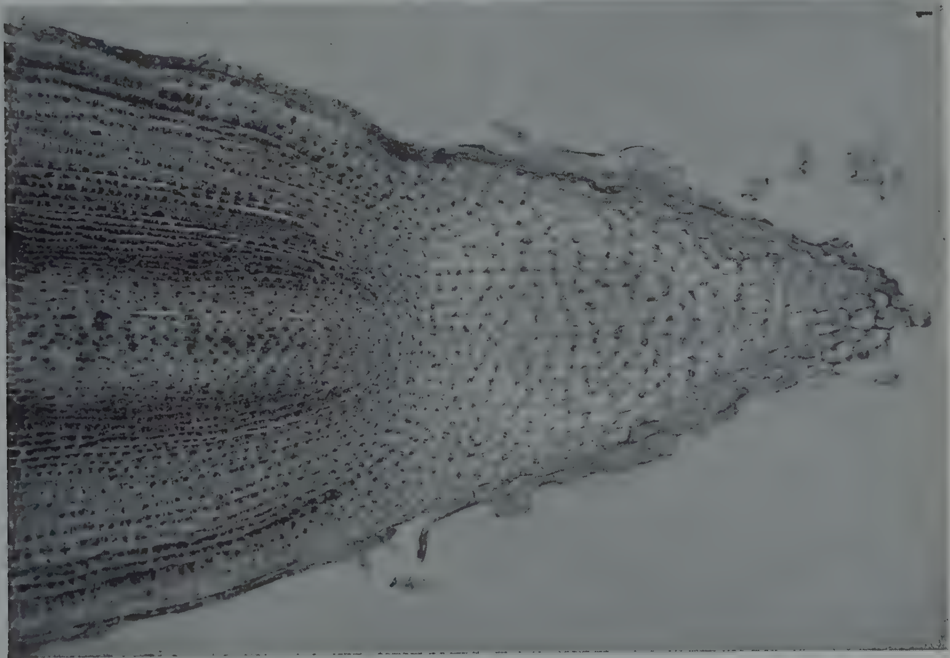
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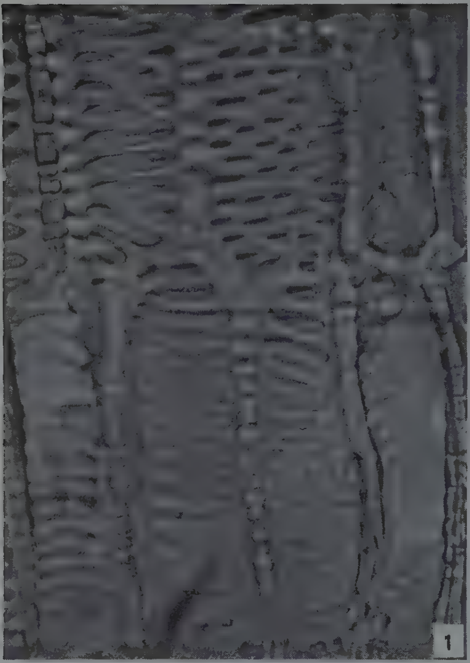

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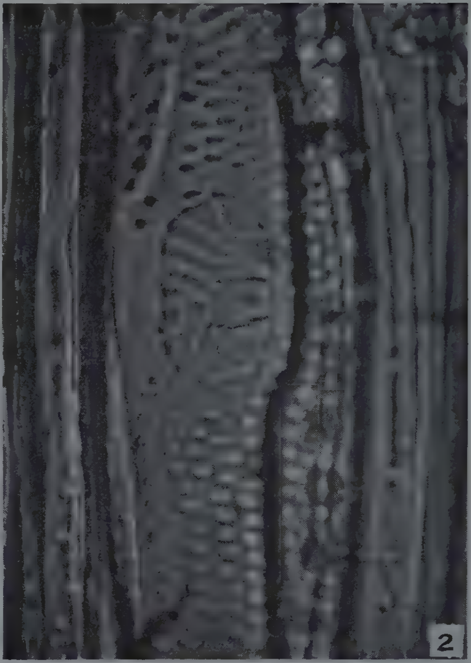

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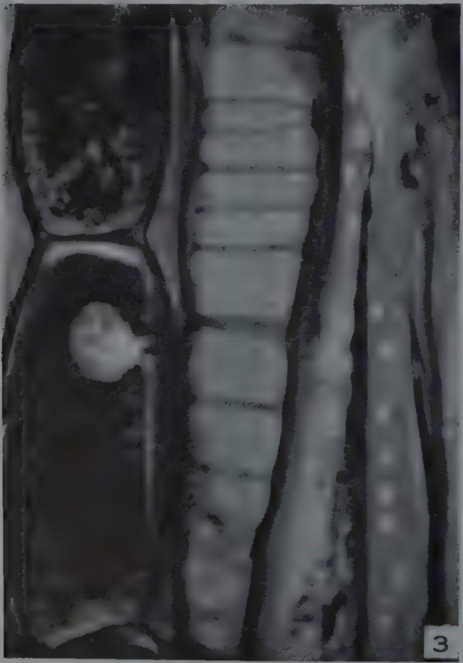

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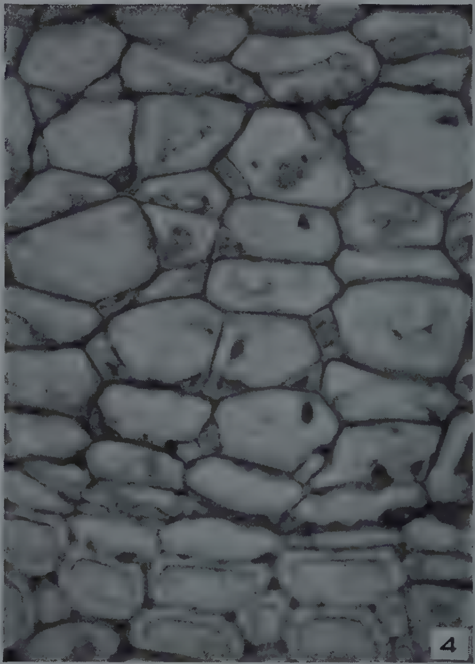

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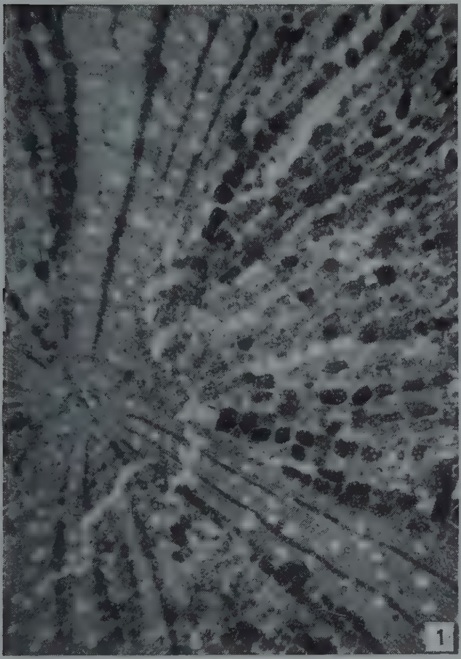

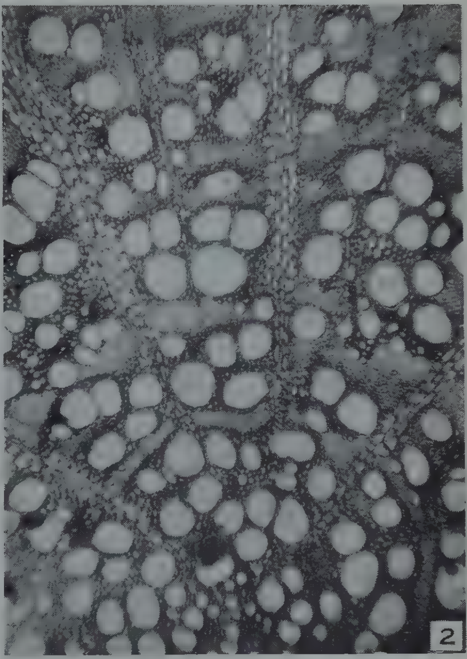

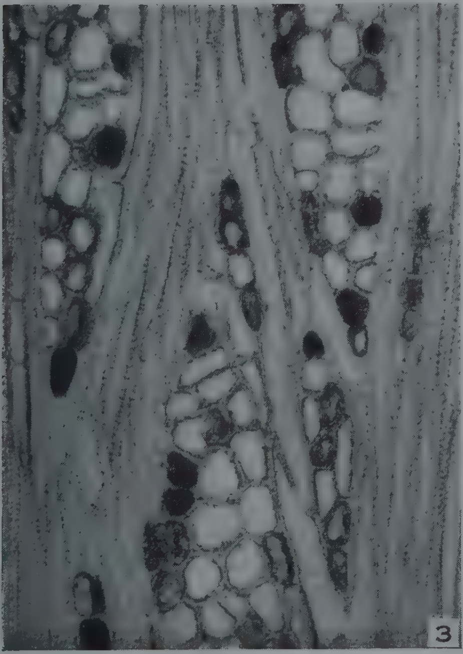

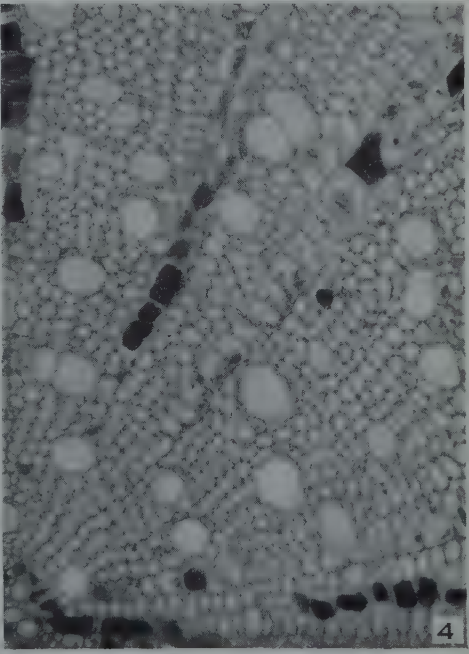

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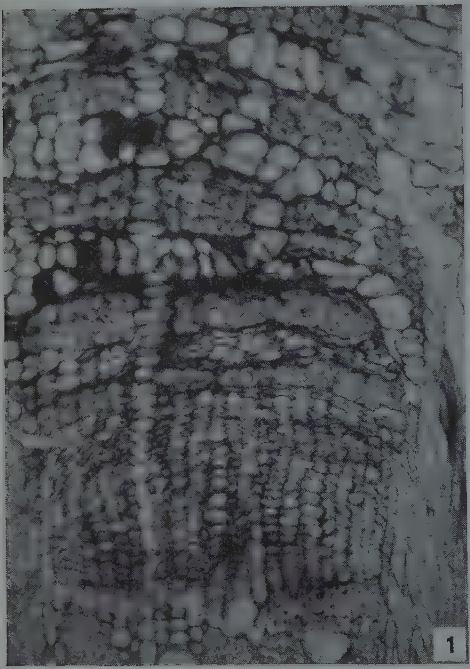
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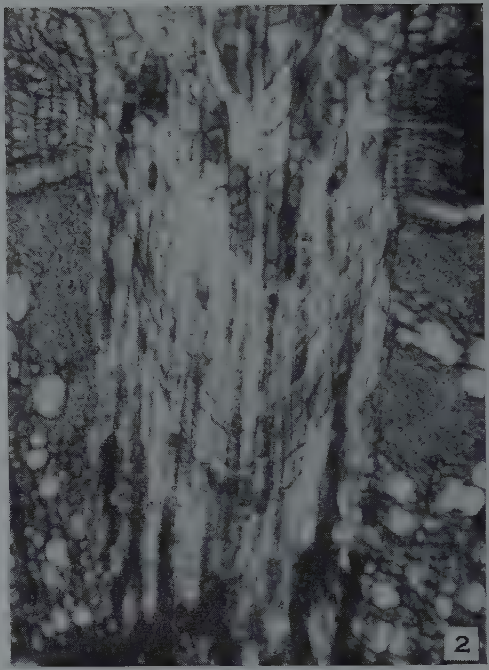
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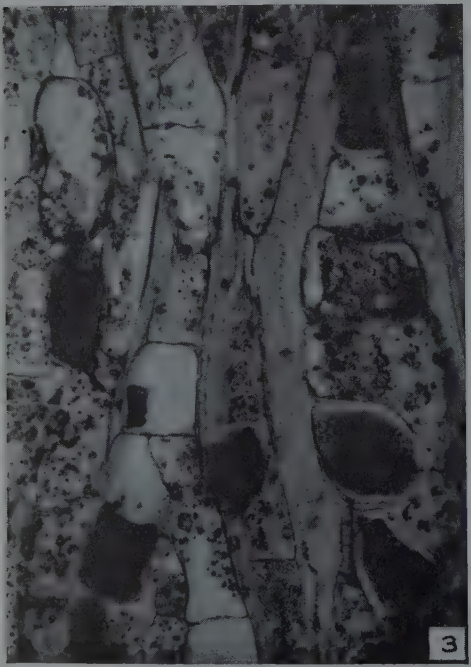
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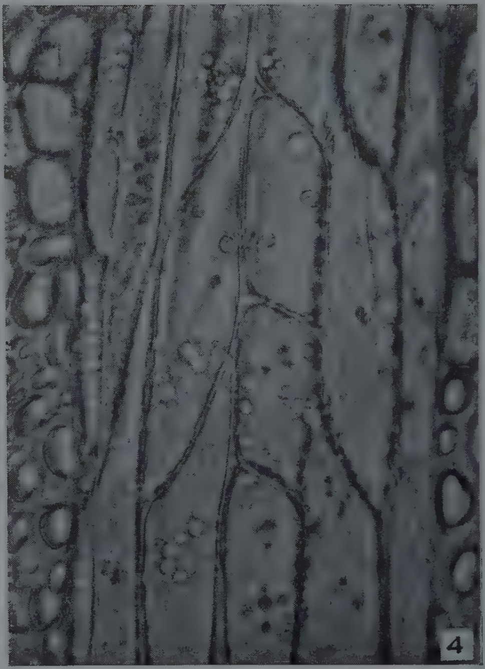
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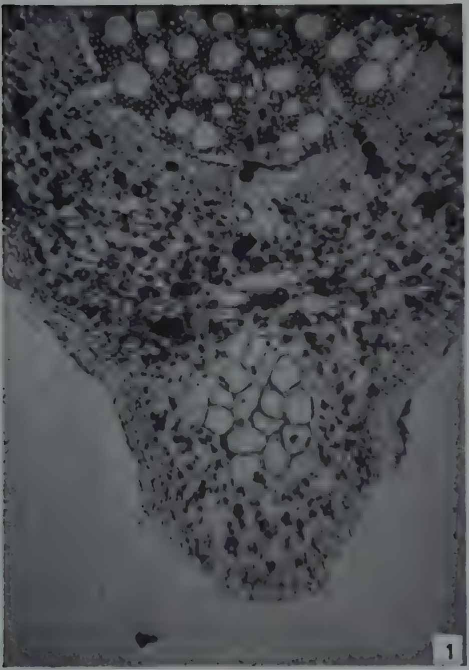
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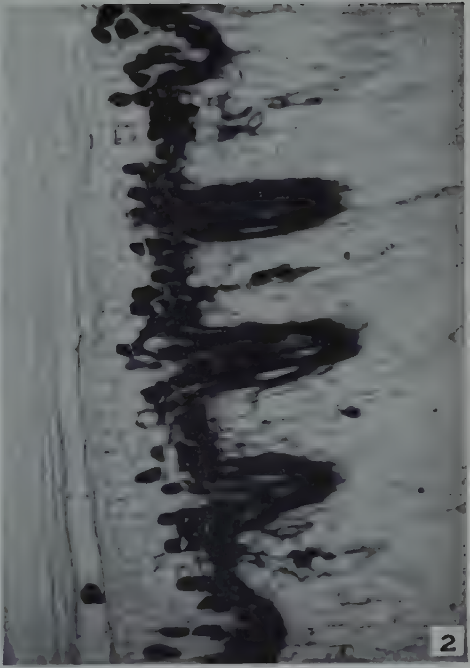
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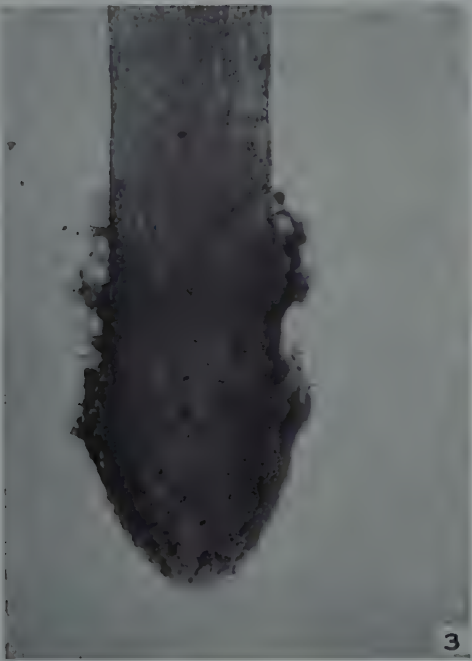
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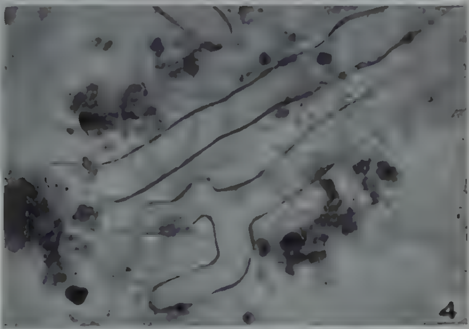
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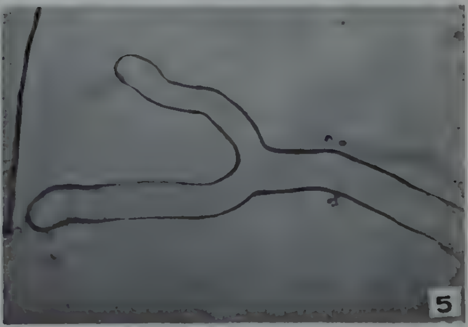
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Plate 5

Fig. 1.—*Hakea sericea*. Median longitudinal section of primary root. ×95.

Fig. 2.—*Banksia marginata*. Longitudinal section of primary root. ×95.

Plate 6

Fig. 1.—*Banksia serrata*. Radial longitudinal section of tap-root. Scalariform bordered pits. ×620.

Fig. 2.—*Telopea oreades*. Radial longitudinal section of tap-root. Reticulate perforation plate. ×920.

Fig. 3.—*Persoonia juniperina*. Tangential longitudinal section of tap-root. Compound sieve plate. ×750.

Fig. 4.—*Conospermum mitchellii*. Transverse section of tap-root. Sieve elements and companion cells. ×650.

Plate 7

Fig. 1.—*Isopogon ceratophyllus*. Transverse section of tap-root. ×50.

Fig. 2.—*Hakea sericea*. Transverse section of tap-root. ×120.

Fig. 3.—*Adenanthos terminalis*. Tangential longitudinal section of tap-root. Splitting of medullary rays. ×120.

Fig. 4.—*Conospermum mitchellii*. Transverse section of tap-root. ×120.

Plate 8

Fig. 1.—*Hakea sericea*. Transverse section of lateral root. Phloem. ×120.

Fig. 2.—*Hakea sericea*. Transverse section of lateral root. ×120.

Fig. 3.—*Persoonia juniperina*. Tangential longitudinal section of tap-root. Sclereids. ×85.

Fig. 4.—*Hakea sericea*. Transverse section of lateral root. Ray cells. ×550.

Plate 9

Fig. 1.—*Conospermum mitchellii*. Transverse section of lateral root. ×125.

Fig. 2.—*Hakea ulicina*. Longitudinal section of proteoid root. ×160.

Fig. 3.—*Banksia collina*. Root cap. ×60.

Figs. 4, 5.—*Banksia collina*. Root hairs. ×625.

Appendix I

SPECIES KNOWN TO FORM PROTEOID ROOTS

(*a*) *Victorian Species Collected in the Field*

Adenanthos terminalis R.Br.
Banksia collina R.Br.
B. integrifolia L.
B. marginata Cav.
B. ornata F.Muell.
B. serrata L.
Conospermum mitchellii Meiss.
Grevillea alpina Lindl.
G. aquifolium Lindl.
G. australis R.Br.
G. chrysophaea F.Muell.
G. ilicifolia R.Br.
G. lanigera A.Cunn.
G. oleoides Sieb.
G. parviflora R.Br.
G. rosmarinifolia A.Cunn.
G. victoriae F.Muell.
Hakea eriantha R.Br.
H. flexilis F.Muell.
H. pugioniformis Cav.
H. rostrata F.Muell.
H. sericea Schrad.
H. ulicina R.Br.
Isopogon ceratophyllus R.Br.
Lomatia fraseri R.Br.
L. ilicifolia R.Br.
L. longifolia R.Br.
Orites lancifolia F.Muell.
Telopea oreades F.Muell.

(*b*) *Non-Victorian Species Collected in the Field*

Grevillea stenobotrya F.Muell.
Isopogon anemonifolius R.Br.
Petrophila sessilis Sieb.

(*c*) *Species Grown from Seed*

Grevillea robusta Cunn.
Hakea laurina R.Br.
H. leucoptera R.Br.
H. nodosa R.Br.
H. purpurea Hook.
H. suaveolens R.Br.
H. undulata R.Br.
Stenocarpus sp.
Telopea truncata R.Br.

THE FINE STRUCTURE OF THE PITS OF *EUCALYPTUS REGNANS* (F. MUELL.) AND THEIR RELATION TO THE MOVEMENT OF LIQUIDS INTO THE WOOD

By J. Cronshaw*

[*Manuscript received July* 24, 1959]

Summary

Observation in the electron microscope of carbon replicas of the pits of vessels, ray parenchyma cells, fibres, and tracheids of *Eucalyptus regnans* has shown the detailed structure of the pit borders and the pit closing membranes. In all cases in the mature wood the primary wall is left apparently without modification as the pit membrane. Unlike the borders of the pits of fibre tracheids and tracheids, the pit borders of the vessels are not separate; the cellulose microfibrils of a border may be common to several pits. The pit borders of fibre tracheids and tracheids are developed as separate entities and have a structure similar to the pit borders of softwood tracheids. The structure of the secondary wall layers associated with the pits is described and related to the structure of the pits.

The fine structural features of the pits, especially of the pit closing membranes, are discussed in relation to the movement of liquids into wood.

I. INTRODUCTION

The function of the pits of woody elements in allowing the passage of liquids between the cells has long been recognized. The gross anatomy of the pits has been fully described but until quite recently little was known of their fine structure or of the mechanism allowing the movement of liquids between cells. In order to explain some of the problems encountered, a knowledge of the fine structure of the pits and especially of the pit closing membrane is essential.

Electron microscopic studies of the inner and outer surface of mature softwood tracheids have shown the detailed structure of the bordered pits (Liese 1951; Harada and Miyazaki 1952; Liese and Fahnenbrock 1952; Liese and Hartmann-Fahnenbrock 1953). The circular pit border is laid down on the primary wall, which is in turn partly covered by the layers of the secondary wall. Thus on the lumen side of the cell wall the cellulose microfibrils of the innermost wall layer are displaced laterally in the region of the pit aperture. On the inside of the pit border, however, the microfibrils run in a circular arrangement around it. The two primary walls of adjacent cells, plus the intercellular layer, differentiate to form a central torus which is supported by radial strands consisting of single microfibrils or bundles of microfibrils. The existence of the holes between these radial strands has also been described following filtration experiments with particle suspensions (Bailey 1913; Frenzel 1929; Liese 1956).

The hardwoods present a different picture, complicated by the heterogeneous nature of the wood. Corresponding with the different types of element there are many variations in pit structure. A major difference from the pits of the softwoods is that in general the pit membrane does not develop a torus, although there is still some doubt about this point (Esau 1953; Huber and Merz 1956; Jane 1956).

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* Division of Forest Products, C.S.I.R.O., Melbourne.

By means of the electron microscope and replica techniques, it has been shown that in the intervascular bordered pits of *Betula*, *Fagus*, *Populus*, and *Salix* the structure of the pit border closely resembles that of conifers (Muhlethaler 1953; Harada 1954; Liese 1957). The microfibrils are arranged around the pit aperture on the cell lumen side, and in the pit chamber they are arranged in the form of two oval half-curves (Liese 1957). The pit membrane is developed without visible openings and shows a primary wall texture in which the microfibrils are embedded with encrusting substances. In his study of the walls of differentiating vessels of *Fraxinus*, Bosshard (1952) has shown that the pit borders do not develop separately, but that microfibrils from one border curve round to take part in an adjacent one. Wardrop (1954) has made similar observations in developing vessels of *Ulmus*.

In the present investigation the carbon replica technique has been applied to a determination of the fine structure of pits in fibres, tracheids, vessels, and ray parenchyma cells of *Eucalyptus regnans* F. Muell. This work forms a part of the fundamental investigation of structural features influencing the penetration of liquids into wood.

II. Materials and Methods

The material used in the present investigation was sapwood taken from a 10-year-old tree of *E. regnans* collected from Toolangi, Vic.

Carbon replicas were made either of untreated wood, or of material sectioned at 8 μ and then extracted with chlorine water followed by dilute sodium hydroxide. Impressions of the wood in "Perspex" were shadowed with uranium at an angle of 12° to the specimen surface before evaporation of the carbon. The carbon replicas were examined in an R.C.A. type E.M.T. electron microscope. Other techniques will be described in the relevant sections.

Examination of Electron Microscopic Observations

In describing the electron microscopic observations it is convenient to consider separately the various types of elements which form the woody tissue and their corresponding pits.

(*a*) *Vessels*

The vessels *in situ* have an average tangential diameter of about 160 μ. The walls are comparatively thin and are almost completely covered with pits. The pits are of two main types. Those which connect the vessels to the tracheids are bordered and circular (Plate 1); those which connect the vessels to the ray parenchyma cells are simple to half-bordered and are more irregular in shape (Plate 3, Fig. 3). The pit borders are laid down on the primary wall. In the border the cellulose microfibrils are in a more or less circular arrangement, delimiting an area of primary wall which will be left as the pit closing membrane (Plate 1, Fig. 1). Unlike the borders of the pits of the fibres and of conifer tracheids, the microfibrils from one pit border may be common to several pits (Plate 2, Fig. 1). The pit membrane in the mature vessels has a primary wall texture in which the microfibrils are randomly arranged in a fairly loose network which is encrusted with other substances (Plate 1, Fig. 1; Plate 3, Fig. 3). The pit membrane in unextracted samples is often covered with a thick deposit of amorphous material which has a wart-like texture (Plate 1, Fig. 2).

The lumen side of the vessels is covered by a warty membrane. However, at the position of the pit apertures there is a heavy deposition of material similar to that found on the pit membrane (Plate 2, Fig. 2).

(*b*) *Ray Parenchyma*

The pits of the ray parenchyma cells are large simple pits and are quite numerous over the surface of the wall.

From the lumen side of the cell the wall may be thickened, with the microfibrils following a transverse direction (Plate 4, Fig. 1). Through the large apertures the pit membrane is visible. It appears flat and has randomly arranged microfibrils. From the outside of the cell it is apparent that the primary wall having randomly arranged microfibrils is continuous over the pit forming the pit membrane (Plate 4, Fig. 2).

(*c*) *Vasicentric Tracheids*

The tracheids of *E. regnans* are basically similar to softwood tracheids. The pits are quite numerous and are in vertical rows. The pit border is laid down on the primary wall, delimiting a circular area. The microfibrils of the border appear to follow a circular path (Plate 5, Fig. 2; Plate 6, Fig. 1). Each pit border is complete in itself and microfibrils do not appear to run from one border to the next or from the border to one of the wall layers. The pit closing membrane is similar in structure to surrounding areas of primary wall, the network of microfibrils of the primary wall being continuous across the pit (Plate 5, Figs. 1 and 2). This network of microfibrils is encrusted with amorphous material. There is no thickening of the pit closing membrane but in some cases there is a tendency to a radial arrangement of the microfibrils (Plate 5, Fig. 1). On the lumen side of the tracheid the microfibrils of the various wall layers are displaced laterally in the region of the pit aperture, which is elliptical in shape (Plate 6, Fig. 2).

(*d*) *Fibre Tracheids*

The wood fibres have far fewer pits than the tracheids. The pits are scattered along the length of the fibre and are usually a considerable distance apart. The fibre pits are smaller in size than the tracheid pits, corresponding with the difference in size of the elements. Except for the difference in size the pits are similar in fine structure to the pits of the tracheids (Plate 7; Plate 8). The pit border again appears as a circle of microfibrils laid down on the primary wall, delimiting an area which is left as the pit closing membrane, the microfibrils of which have a random arrangement, there being no tendency for them to be radial. They are, however, encrusted with amorphous material, although as with the other pit closing membranes that have been described there is no central thickening or torus.

The secondary wall layer S2 encroaches over the border, and the major axis of the elliptical pit aperture is always in the same direction as the microfibrils of the wall layer S2. The layer S3 then lies on the lumen side of the cell (Plate 8, Fig. 2).

III. THE STRUCTURE OF THE SECONDARY WALL LAYERS ASSOCIATED WITH THE PITS

The borders of the various types of pits described are laid down on the primary wall. They are thus the first evidence of secondary wall formation in the cell. Except in the case of the vessels, the borders do not form a complete layer over the inside of the cell but are distinct entities and may, in certain cases, be dislodged from the other wall layers (Plate 8, Fig. 1). In the pit borders the microfibrils appear to follow a circular path, but it is difficult to follow the course of a single microfibril for any distance owing to its interweaving. The short length which may be observed appears to be in a tangential direction to the general circular shape of the border. It has been pointed out by Liese (1957) for beech, that at two points opposite on the pit border the tangential microfibrils appear to cross. This is also the case in *E. regnans* and may be observed in Plate 7, Figure 1, and Plate 8, Figure 1. In the case of the vessel bordered pits, the pit borders form a more or less continuous layer of the cell wall, and parallel sets of microfibrils may run from one border to the next (Plate 2, Fig. 1).

After the borders have been formed on the inside of the fibres and tracheids, the well-recognized layers of the secondary wall are laid down. These layers are continuous over the inside of the cell, and whilst they may eventually cover the border, the microfibrils of the various layers are arranged around the pit aperture and never encroach over it. It may be seen that the layer S1 or first-formed secondary layer has a crossed fibrillar structure (Plate 7, Fig. 2). The aggregates of parallel microfibrils run in two directions which are approximately at right angles to one another. There is some evidence that the two directions may be in separate lamellae, as in Plate 7, Figure 1. One direction is at one side of the pit border and a second direction at a large angle to it is at the other. The two directions form flat helices to the fibre axis but do not appear to cover the pit borders.

In the layer S2 the microfibrils are parallel to one another and form a steep helix to the fibre axis. This layer covers the pit border, and the microfibrils are arranged around the pit aperture. In this layer a fan-like arrangement of the microfibrils has been observed, similar to those described by Harada, Miyazaki, and Wakashima (1958) for softwood tracheids (Plate 3, Fig. 2). There is also evidence that the transition lamellae described by Harada, Miyazaki, and Wakashima (1958) for *Picea* and *Pinus* may be present in *Eucalyptus*. In Plate 3, Figure 1, it can be seen that between the layers S2 and S3 is a transition layer in which the microfibrils are in a direction approximately between the directions of the microfibrils in the other two layers.

The last-formed layer (S3) of the secondary wall covers the whole of the inside of the cell except the pit apertures (Plate 8, Fig. 2). The microfibrils of this layer appear to be in two directions at a small angle to one another. In some cases the layer may be very thin, and in such specimens it does not show as a birefringent layer in cross sections. Nevertheless, the layer is always present and the microfibrils of the two directions follow a slow helical path to the axis of the cell. The microfibrils cannot be followed for any great distance and present a sheafing appearance (Plate 6, Fig. 2; Plate 8, Fig. 2).

IV. Relation of Structural Features to the Movement of Liquids

Early attempts to define the penetration path of liquids into wood were initiated when Bailey (1913) passed suspensions of carbon particles through softwood samples. Later Frenzel (1929) performed similar experiments, using colloidal gold of known particle size. The method was further refined by Liese (1956), who made electron microscopic determinations of the particle size of suspensions which had filtered through samples of softwood. From these experiments and from observations of the pit membrane in the electron microscope it was obvious that there were definite holes in the pit closing membrane of softwoods. This was doubted for a time by some workers (Frey-Wyssling and Bosshard 1953), who used an ultrathin sectioning method, but was later confirmed by a study of the development of the pit membrane (Frey-Wyssling, Bosshard, and Muhlethaler 1956).

In the case of hardwoods, the situation is very different. The vessels appear to present a very easy pathway for the rapid movement of liquids in the direction of the grain of the wood, but a direct flow of liquid through the pits, such as can occur through the pits of softwoods, is unlikely in view of the structure of their closing membranes. Thus movement of liquid in a transverse direction in the wood can take place only with difficulty.

Some preliminary experiments have been carried out to try to determine the possible pathways for the movement of liquid through the wood. A sample of wood 1 cm^3 was cut from fresh sapwood. One end was immersed in a particle suspension and a vacuum applied at the other. Suspensions of colloidal carbon or colloidal gold (640 Å) were observed to pass through the vessels even when the length of wood was increased to 10 cm. Optical microscopic observations of sections cut from the wood revealed that the particles accumulated in the pit chambers but did not cross the pit membranes. When the vessels of the sample were first blocked, e.g. with dental cement, the particles passed into the cut ends of the fibres but again could not pass into adjacent elements. These results are in complete agreement with the electron microscopic observations that the pit membranes appear imperforate. Thus where the vessels of a sample of wood are blocked by natural means, such as tyloses, penetration of the wood by liquids is very difficult.

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Explanation of Plates 1–8

Plate 1

Figs. 1 and 2.—Electronmicrographs of carbon replicas of parts of vessels of *E. regnans*, showing the structure of the pit membrane. Note the accumulation of amorphous material on the pit membrane in Fig. 2.

Plate 2

Fig. 1.—An electronmicrograph of a carbon replica of part of vessel of *E. regnans*, showing the arrangement of the microfibrils in the pit border. Original specimen extracted with chlorine water and dilute caustic soda.

Fig. 2.—An electronmicrograph of a carbon replica of the lumen side of part of a vessel of *E. regnans*. Note the accumulation of amorphous material at the positions of the pit apertures.

Plate 3

Fig. 1.—An electronmicrograph of a carbon replica of the lumen side of part of a fibre of *E. regnans*. The secondary wall layer S3 is torn away to show a transition layer between it and the layer S2.

Fig. 2.—An electronmicrograph of a carbon replica of the lumen side of part of a fibre of *E. regnans*. The layer S3 is torn away, revealing a fan-like arrangement of microfibrils in the underlying layer.

Fig. 3.—An electronmicrograph of a carbon replica of part of a vessel of *E. regnans*. The pit membrane is encrusted with amorphous material.

Plate 4

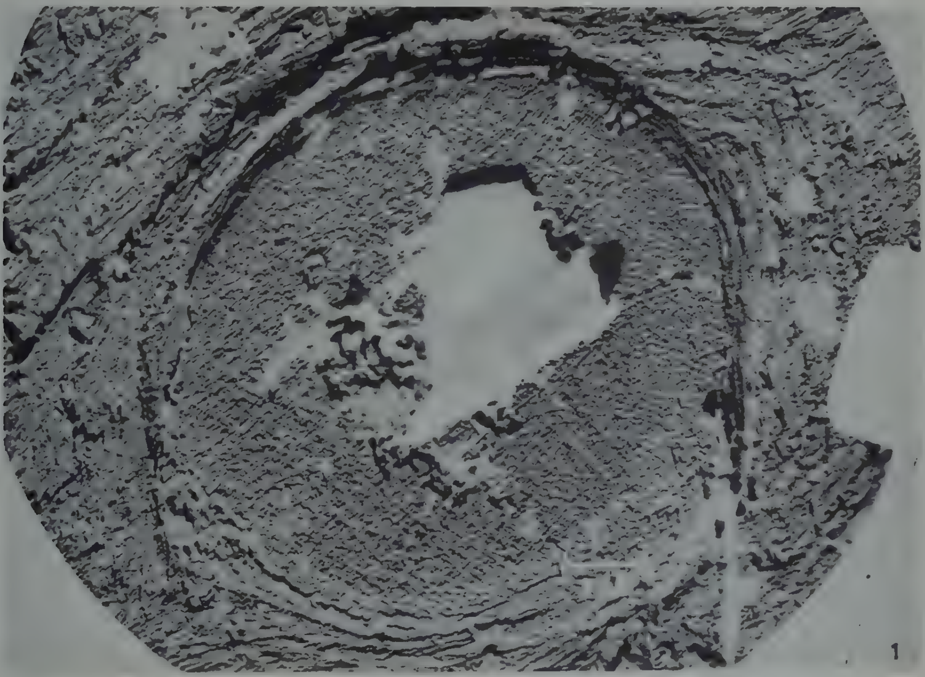
Fig. 1.—An electronmicrograph of a carbon replica of part of the lumen side of a ray parenchyma cell of *E. regnans*. The primary wall structure of the pit membrane is visible through the pit apertures. The original specimen was extracted with chlorine water and dilute caustic soda.

Fig. 2.—Similar specimen to Fig. 1, seen from the outside. The primary wall layer is continuous over the pit apertures.

Plate 5

Figs. 1 and 2.—Electronmicrographs of carbon replicas of parts of tracheids of *E. regnans*, showing the wall texture of the pit membrane. In Fig. 1 there is a tendency for some of the microfibrils of the pit membrane to be radially arranged.

FINE STRUCTURE OF PITS OF E. REGNANS



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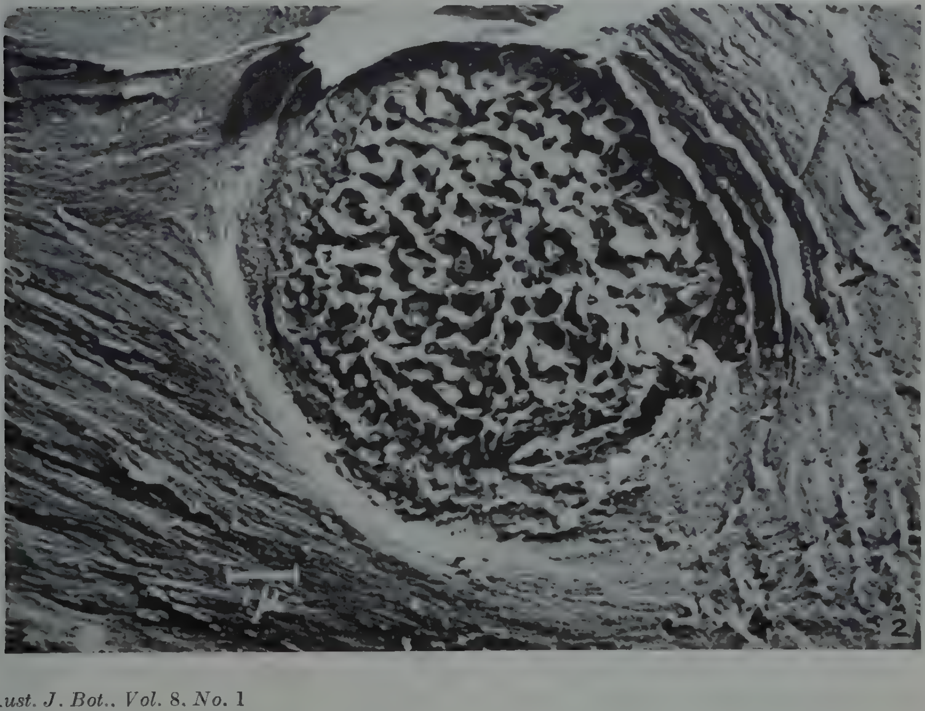

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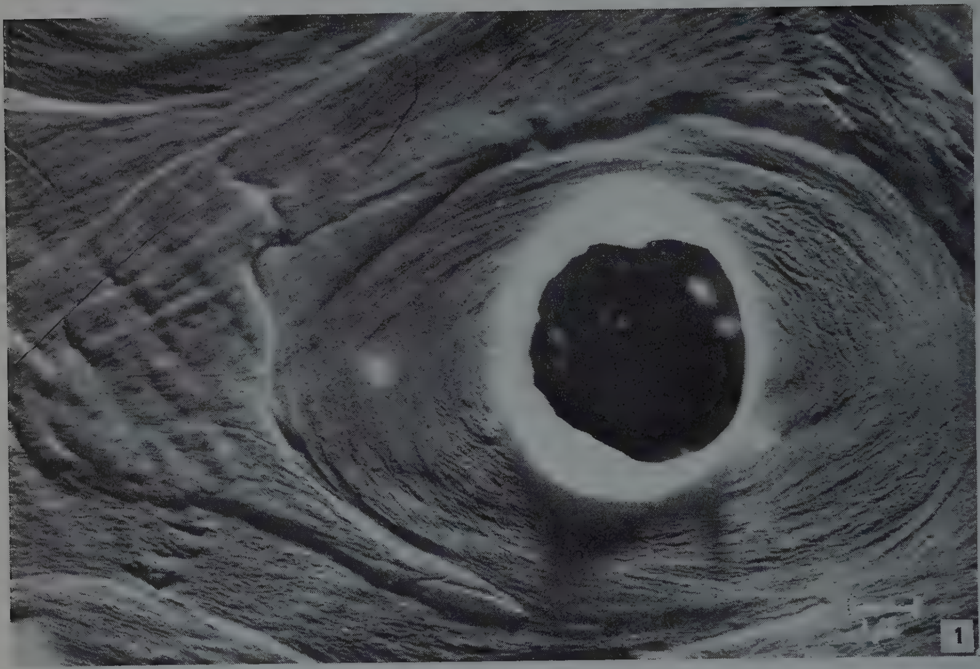

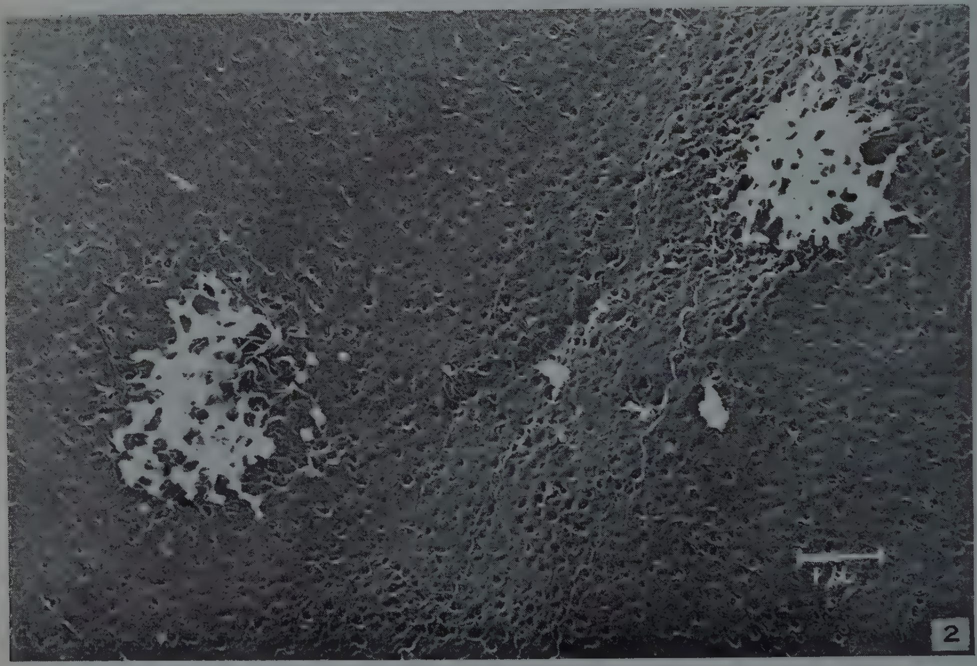

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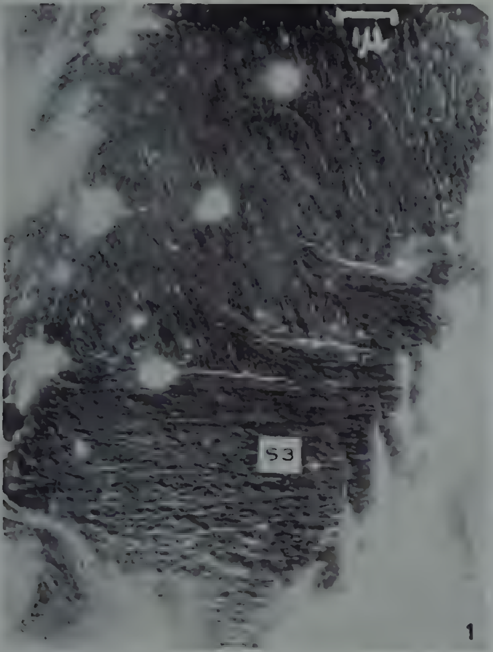

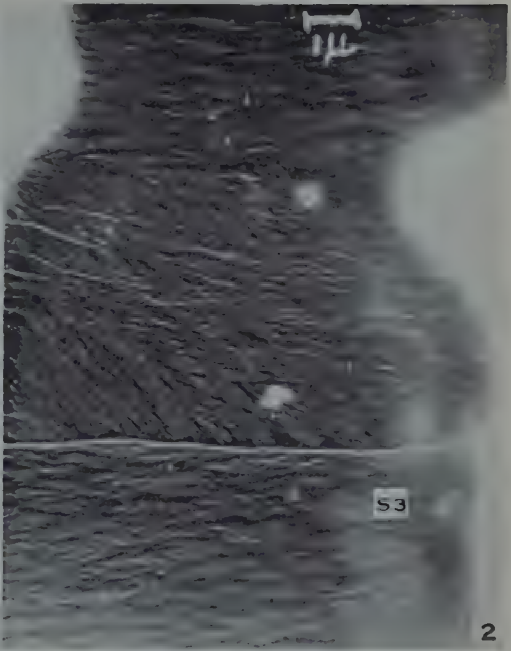

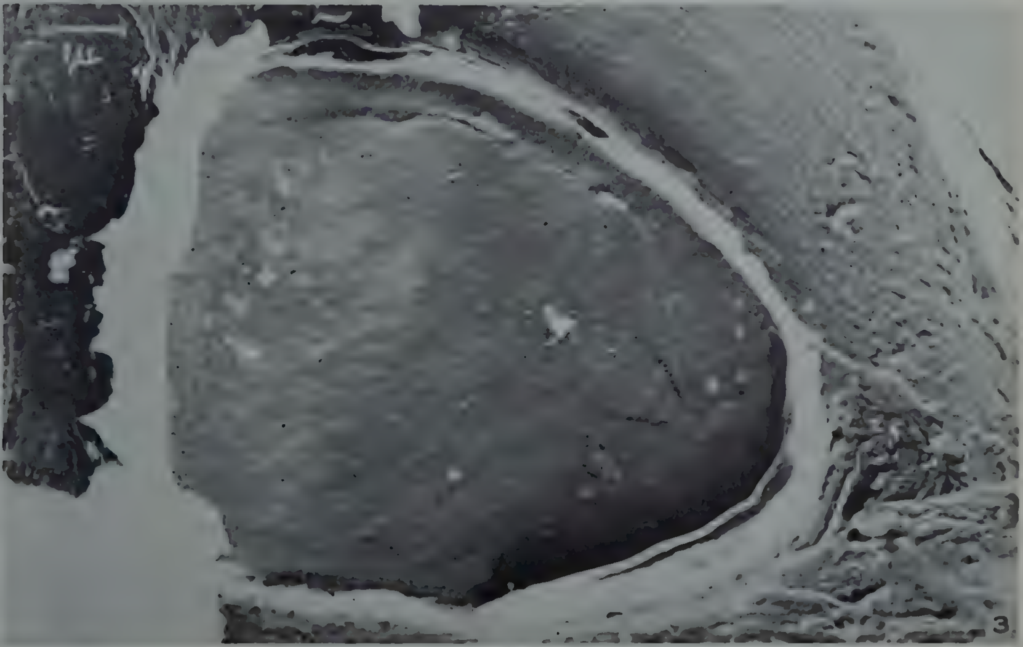

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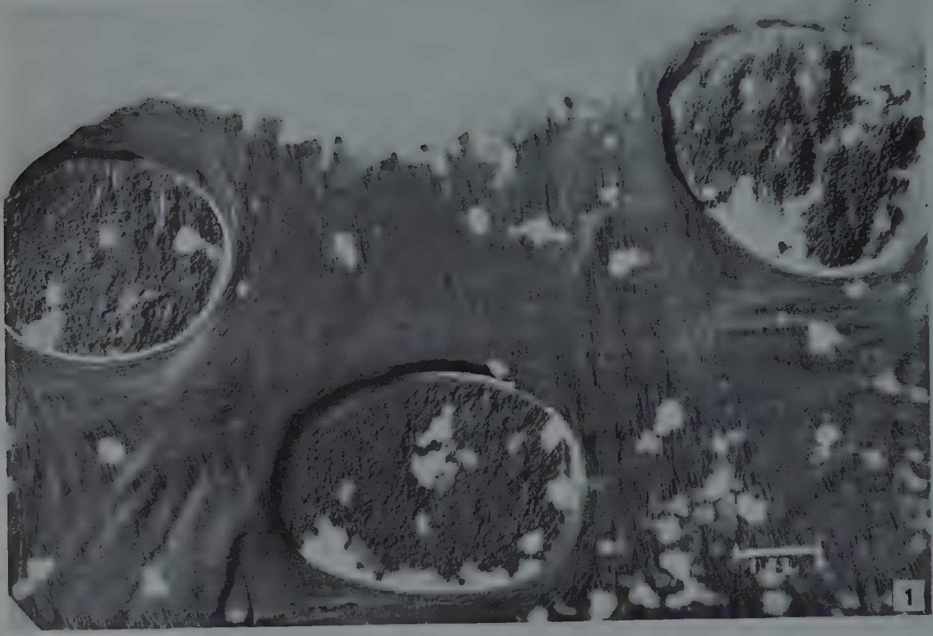

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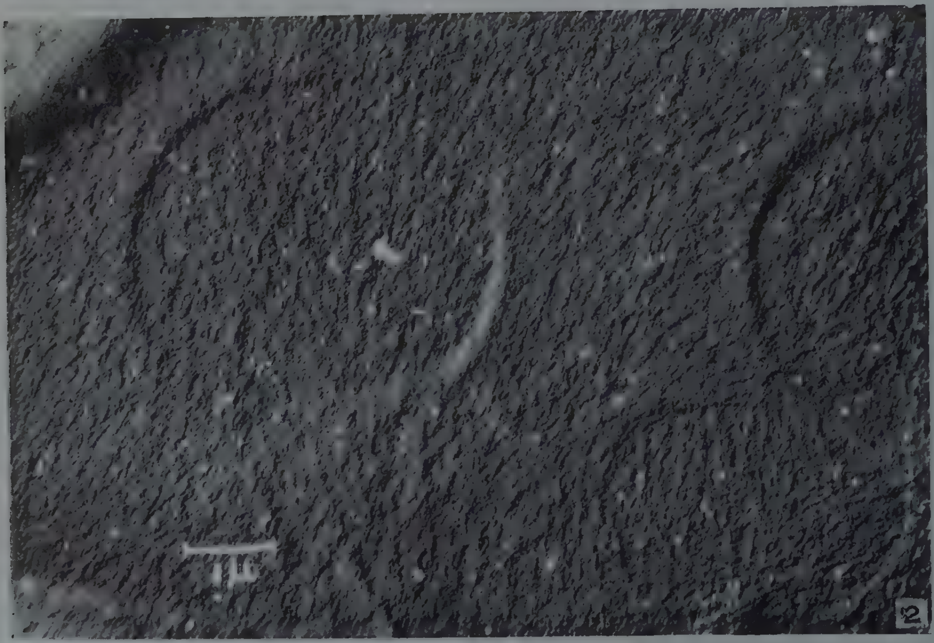

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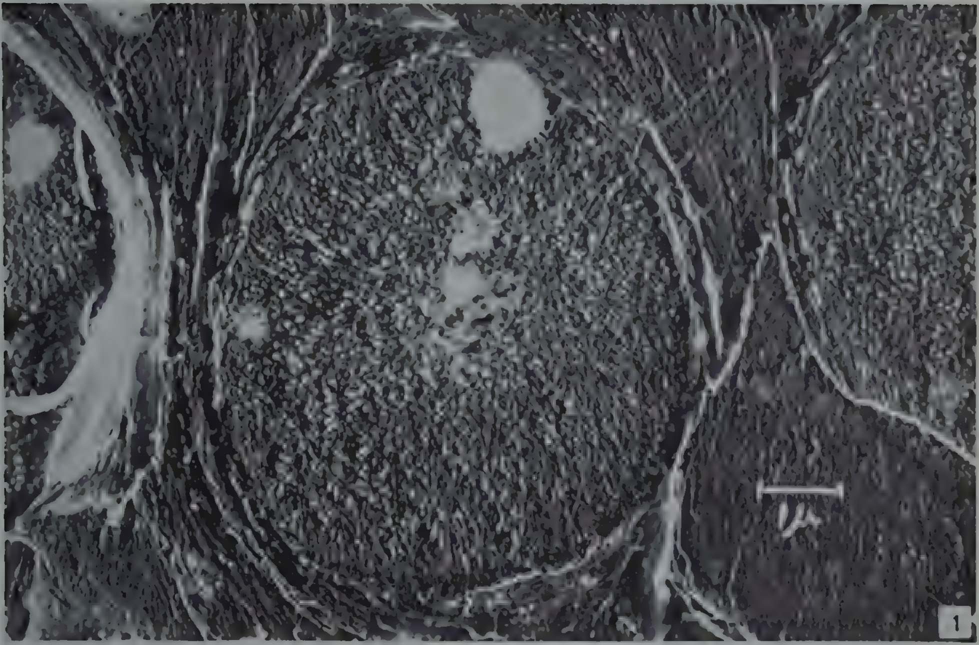

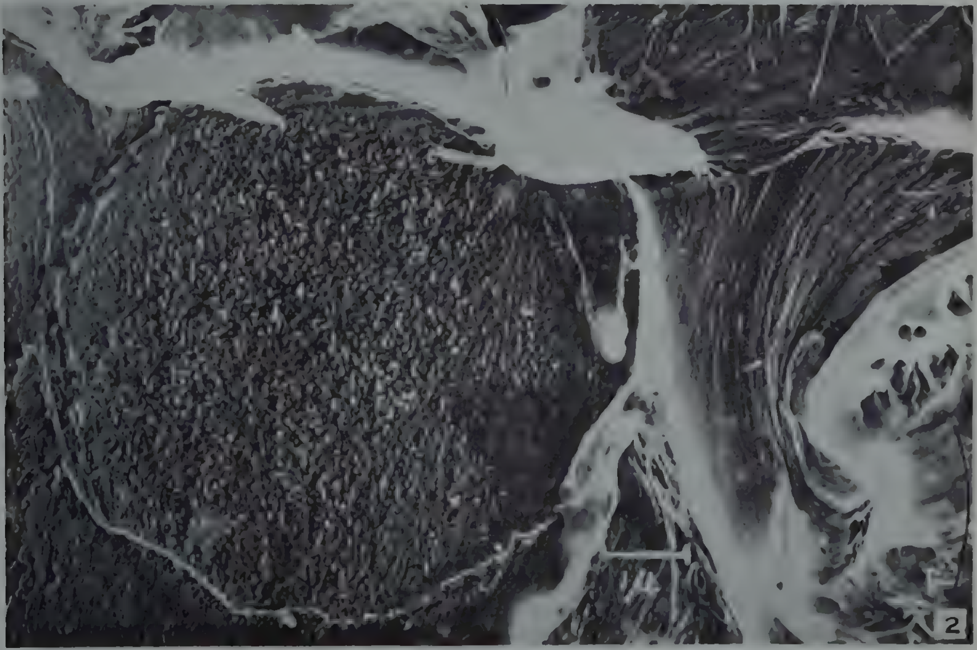

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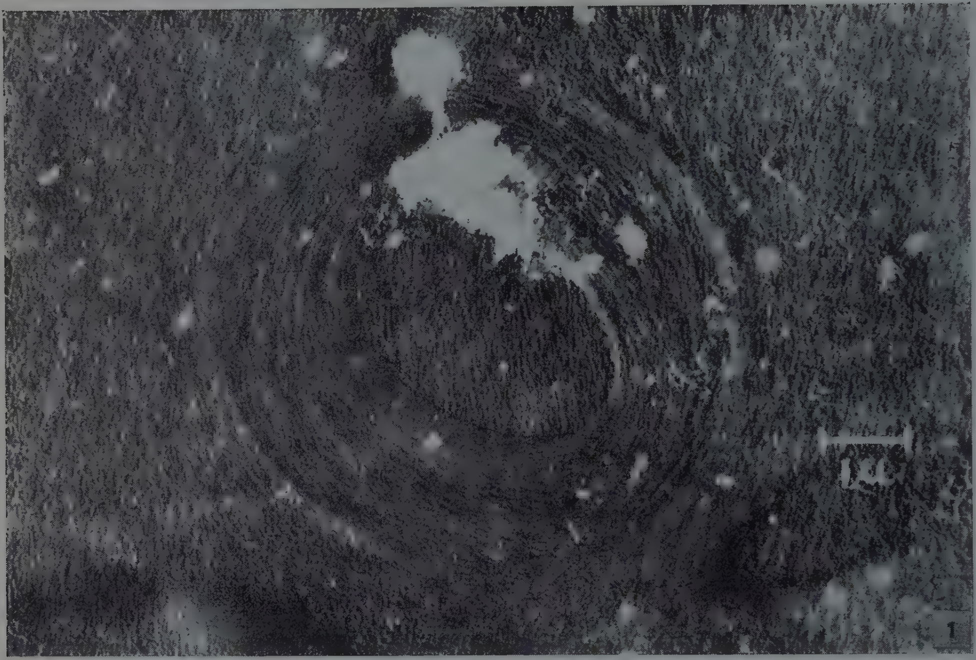

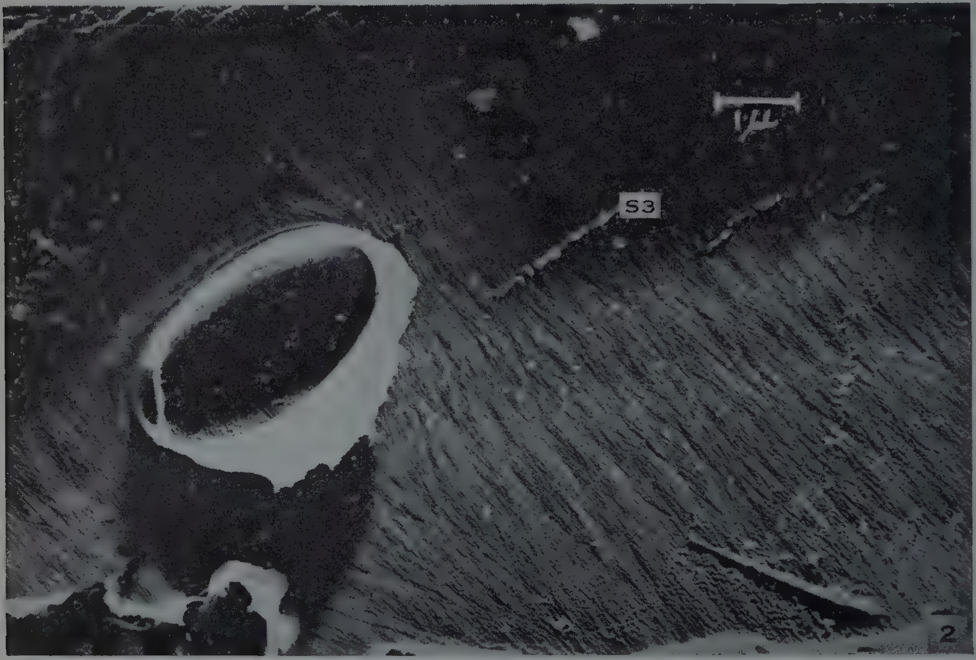

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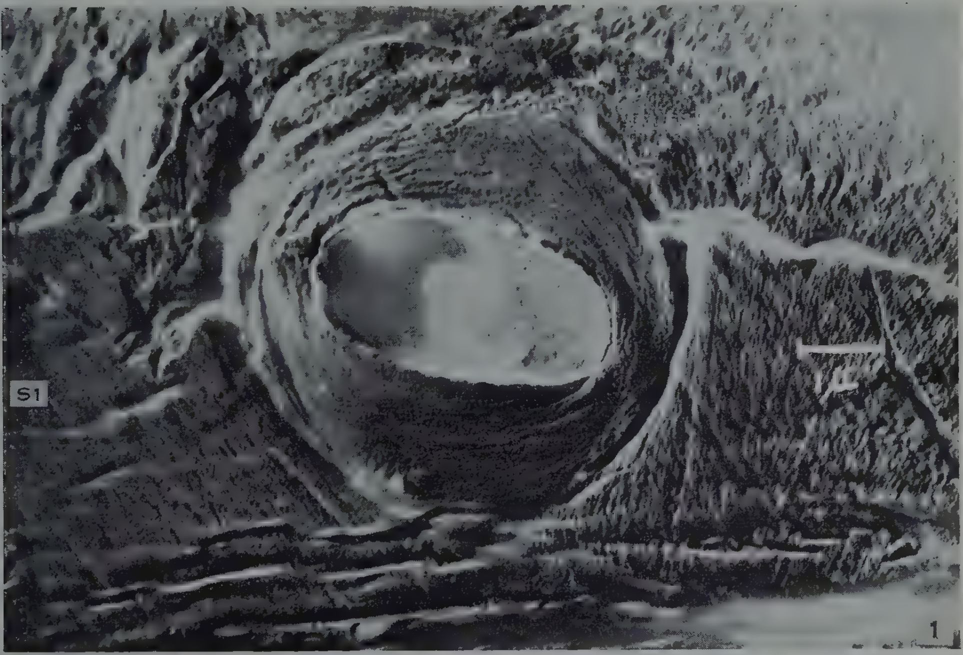

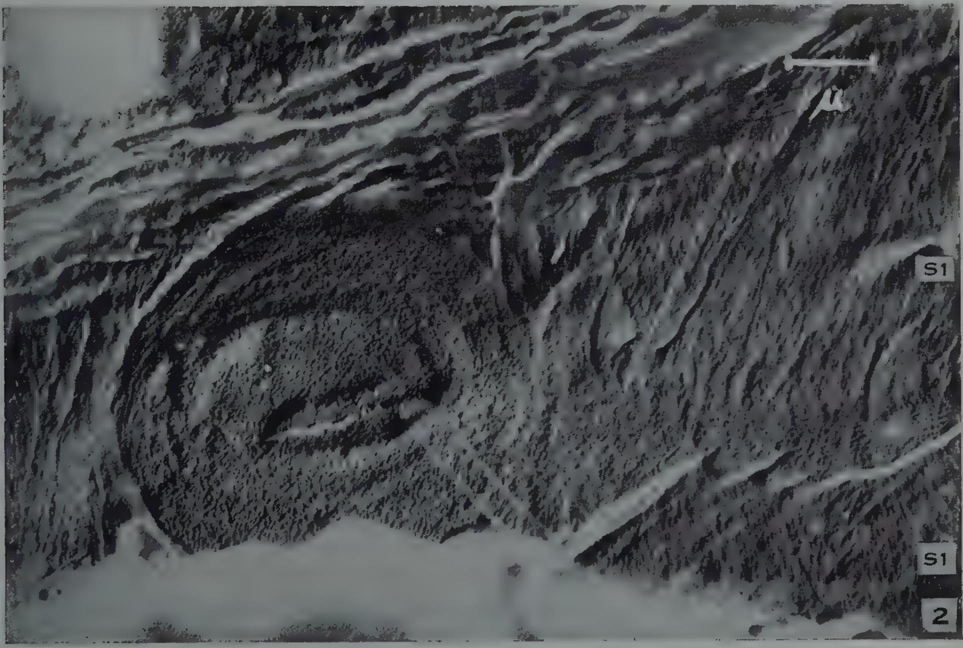

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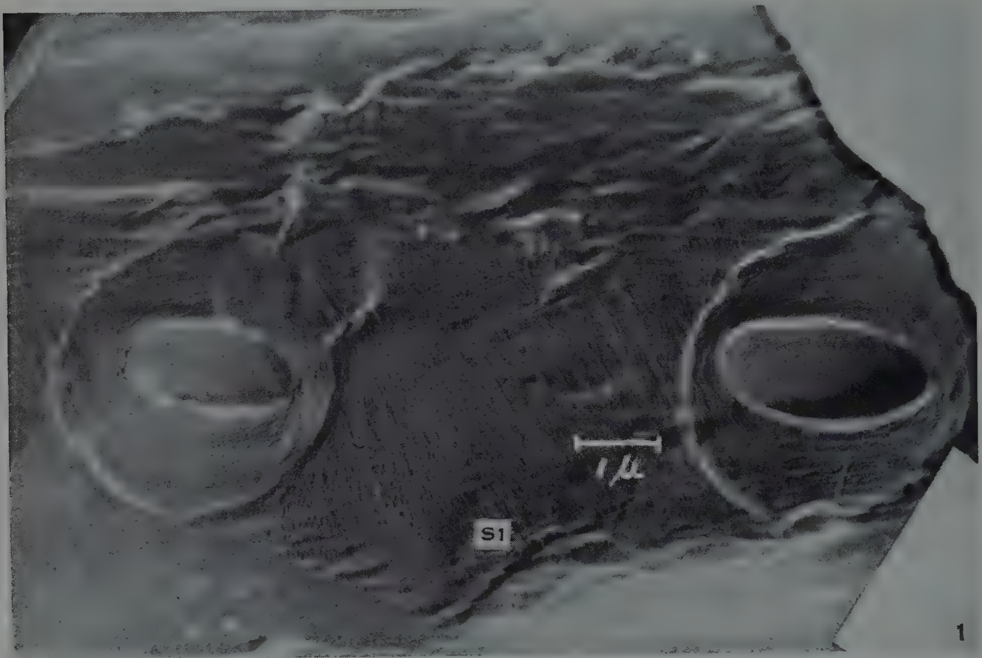

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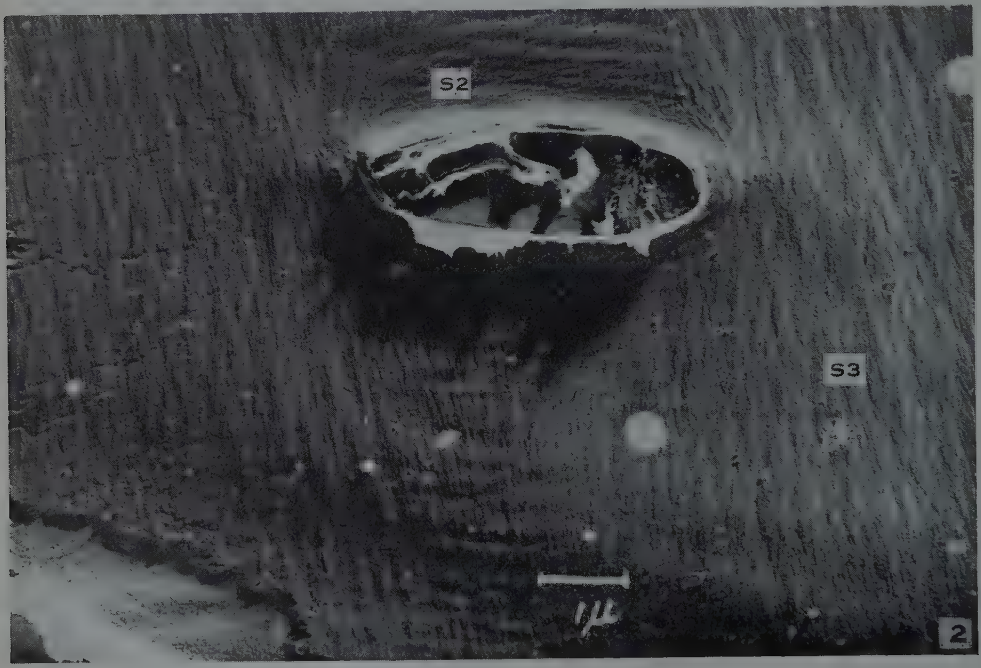

2

Plate 6

Fig. 1.—An electronmicrograph of a carbon replica of part of a tracheid of *E. regnans.* The pit membrane has been torn away, revealing the pit border. Through the pit aperture the texture of the secondary wall layer S3 is visible. Surrounding the pit border is the primary wall. The original specimen was extracted with chlorine water and dilute caustic soda.

Fig. 2.—An electronmicrograph of a carbon replica of a specimen similar to that in Fig. 1, but viewed from the lumen side. The microfibrils of the layer S3 are arranged around the pit aperture.

Plate 7

Fig. 1.—An electronmicrograph of a carbon replica of part of a fibre of *E. regnans.* The pit border is surrounded by the secondary wall layer S1. The original specimen was extracted with chlorine water and sodium hydroxide.

Fig. 2.—An electronmicrograph of a carbon replica of a specimen similar to that shown in Fig. 1. The pit membrane is seen to be continuous with the primary wall. On either side of the primary wall are the S1 layers of adjacent fibres.

Plate 8

Figs. 1 and 2.—Electronmicrographs of carbon replicas of fibres of *E. regnans.* The original specimens were extracted with chlorine water and caustic soda. Fig. 1 shows the secondary wall layer S1 with two pit borders. Fig. 2 shows the specimen from the lumen side; the layer S3 is very thin and reveals the layer S2. The microfibrils of the secondary wall layers are displaced laterally in the region of the pit aperture.

THE DISTRIBUTION AND CYTOLOGY OF THE CHROMOSOME RACES OF *THEMEDA AUSTRALIS* IN SOUTHERN AUSTRALIA

By D. L. Hayman*

[*Manuscript received June* 30, 1959]

Summary

Themeda australis (R.Br.) Stapf is a polyploid complex based on $n = 10$, and diploid, triploid, tetraploid, pentaploid, and hexaploid individuals have been found. Over 98 per cent. of more than 800 individuals examined were either diploid or tetraploid. Some 300 populations, from localities on the Australian mainland below the Tropic of Capricorn, were characterized by their chromosome number and a very clear pattern of distribution was found. Diploid populations occur exclusively on the Eastern Highlands and slopes in southern Victoria and in Tasmania; elsewhere tetraploid populations occur across to Western Australia. Triploid, pentaploid, and hexaploid plants are found as individuals in populations of another chromosome number.

The cytological evidence shows a very close relationship to exist between the constituent genomes of the polyploids.

The significance of the distribution of the chromosome races, the effects of polyploidy, and the implications of this pattern for further studies on the native flora are discussed.

I. Introduction

Themeda australis (R.Br.) Stapf, the commonly known "kangaroo grass", is a member of a small genus of tropical and subtropical grasses. Three taxonomic species of the genus are found on the Australian mainland, and of these *T. australis* is the only one which has a distribution extending into the temperate regions. This species, found in Tasmania, in New Guinea, and in all States on the mainland, is a dominant both of temperate and of subtropical grasslands. Its habitat is exceedingly wide, extending from the banks of seasonal watercourses in central Australia to altitudes up to 5000 ft in the Australian Alps. No other species in the Australian flora has a distribution more extensive than *T. australis*, and very few have one as great. A species with such an extensive range is an attractive one in which to study the genetical and physiological features of adaptation and natural selection.

Preliminary chromosome counts of *T. australis* revealed that the taxonomic species consisted of a number of chromosome races. So far, five chromosome numbers, the diploid, triploid, tetraploid, pentaploid, and hexaploid, have been found. It has been well established that the individual members of such a polyploid series frequently show a distribution pattern which can be related to migration and adaptation (Darlington 1956). Extensive collections from natural populations of *T. australis* have revealed such a pattern in this species. The collections have come predominantly from southern Australia. Insufficient data are available as yet for the areas above the Tropic of Capricorn, and few conclusions can be drawn from the distribution of the populations there.

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This paper describes the cytology and distribution pattern of the members of the polyploid series in southern Australia. It is intended to publish a parallel study for northern Australia when more information becomes available.

II. Methods

Collections of seeds were made personally, or were obtained through other collectors, from a large number of populations of *T. australis*. The populations sampled were predominantly from south-eastern Australia since these were the most accessible. The distribution of the collection sites is a reflection therefore of the ease of collecting, and of the distribution of collectors, rather than that of the species as a whole. The species is frequently restricted to areas which are protected from grazing, such as cemeteries, roadways, and railway lines. Such areas are hardly natural and are susceptible to interference by man. Wherever possible, therefore, collections were obtained from different populations close together, so that a measure of the consistency of the results could be obtained. Each population was characterized by a number of individuals, usually three.

The chromosome counts were made on the root tips of seedlings pretreated with α-bromonaphthalene for $1\frac{1}{2}$ hr, fixed in ethanol–acetic acid (3 : 1), hydrolyzed in N hydrochloric acid at 60°C for 6 min, and stained in aceto-orcein. Meiosis was examined in the pollen mother cells of plants grown in a grass garden.

The germination of the seeds was generally poor. The most successful technique was to keep them in a domestic refrigerator for 48 hr and then germinate them on filter paper moistened with a 0·1 per cent. solution of potassium nitrate (Frith 1957).

III. Cytological Features of the Chromosome Races

The basic chromosome number of *T. australis* is $x = 10$, which is in agreement with the known chromosome numbers of other species of the genus (Table 1).

The chromosomes of *T. australis* are too small to permit an accurate analysis of chromosome morphology in root tip cells; further, this makes difficult the interpretation of meiotic configuration and the determination of chiasma frequencies in the polyploid forms.

During the study the somatic chromosome numbers of more than 800 plants from over 300 populations were determined. Some 200 of these were polyploids, and of these about 95 per cent. were tetraploid. Although the preparations obtained were not always sufficiently clear to determine the chromosome number exactly, I believe that no more than 10 per cent. of the tetraploid plants were monosomic or polysomic. This element of uncertainty is absent from the diploid counts, where accurate identification of the chromosome number was always possible. It can only be stated definitely therefore that no accessory chromosomes have been seen in the diploid material.

The details of metaphase pairing, and pollen grain size, in representatives of each chromosome number are summarized in Table 2 (see also Plates 1 and 2). These are based on a minimum of 20 cells, except for the hexaploid data, which are based on eight cells.

The data on chromosome pairing in the triploid and higher polyploids agree in showing a relatively high frequency of multivalents. This frequency of multivalents is certainly reduced in the tetraploids by the low chiasma frequency, which is slightly more than one per potential bivalent.

TABLE 1

CHROMOSOME NUMBERS IN THE GENUS THEMEDA

Species	2*n*	Authority
T. arguens	20	Avdulov (1931) Hayman (unpublished data)
T. avenaceae	40	Hayman (unpublished data)
T. australis	20, 21, 22, 23, 25, 30, 36, 39, 40, 41, 50, 59, 60	Hayman (this paper)
T. cymbaria	20	Raman *et al.* (1959)
T. japonica	80	Tateoka (1954)
T. quadrivalvis	40	Mehra (1955) Hayman (unpublished data)
T. triandra	20, 22, 30, 40, 45, 49, 50, 51, 53, 54, 56, 60, 68, 71	Gluckman (1951)
	80	Celarier and Harlan (1954)
T. trimula	80	Mehra (1955)

There is a slight reduction in the frequency of chiasmata per potential bivalent with an increase in chromosome number from $2n = 20$ to $2n = 40$. This could be the result of "diploidization", that is, the selection of those plants with a tendency to form bivalents rather than multivalents.

Pollen grain size has usually been found a reliable means of distinguishing between diploid, tetraploid, and hexaploid forms. However, a diploid plant from Naracoorte, S.A., had pollen grains of such a size that they would be confused with the pollen grains from tetraploid plants.

Structural hybridity has not been observed in *T. australis*. No bridges and fragments were found at anaphase I or II in the plants examined. No interchange configurations were found in the diploid, and it is assumed that none of the multivalents seen in the polyploids are due to heterozygosity for an interchange, although critical evidence of this is lacking.

The univalents of the pentaploid plant ($2n = 50$) and of the aneuploid plant ($2n = 39$) both showed evidence of neocentric regions when they were orientated on the metaphase plate at the first division of meiosis (see Plate 2, Fig. 2). The true centromere apparently fails to divide, and proximal or distal regions of all four chromatid arms, or two of the four chromatid arms, become orientated towards the poles and chromosome movement is initiated there. The chromosomes appear similar to those described in certain *Phalaris* hybrids (Hayman 1955). Although univalents commonly occurred at meiosis in the triploids, and in the tetraploids, no evidence of neocentric activity was found in them. This suggests that there may be specific genetic factors required for the production of these neocentromeres,

TABLE 2

CYTOLOGICAL FEATURES OF REPRESENTATIVES OF THE CHROMOSOME RACES OF THEMEDA AUSTRALIS

Locality and Chromosome No.	Mean Freq. of Chiasmata per Cell	Average Number of Multivalents per Cell				Range of Multivalents per Cell				Mean Pollen Grain Dia. (μ)
		III	IV	V	VI	III	IV	V	VI	
$2n = 20$										
Omeo, Vic.	13·6	—	—	—	—	—	—	—	—	36·0
Croydon, Vic.	14·2	—	—	—	—	—	—	—	—	42·0
Ross, Tas.	15·8	—	—	—	—	—	—	—	—	38·0
Guyra, N.S.W.	17·1	—	—	—	—	—	—	—	—	38·0
Bathurst, N.S.W.	16·0	—	—	—	—	—	—	—	—	40·4
Emerald, Qld.	15·6	—	—	—	—	—	—	—	—	39·2
Canberra, A.C.T.	15·2	—	—	—	—	—	—	—	—	40·8
Naracoorte, S.A.	14·6	—	—	—	—	—	—	—	—	49·2
$2n = 30$										
Uranquinty, N.S.W.:										
Plant A	18·5	3·5	—	—	—	(2–6)	—	—	—	—
Plant B	18·5	5·5	—	—	—	(3–8)	—	—	—	—
$2n = 39$										
Barossa Valley, S.A.	25·4	1·0	2·5	—	—	(1–3)	(1–5)	—	—	—
$2n = 40$										
Mt. Lofty Ranges, S.A.	26·7	0·5	1·4	—	—	(0–1)	(0–3)	—	—	49·2
Barossa Valley, S.A.	26·0	0·1	2·3	—	—	(0–1)	(1–4)	—	—	51·2
Springhurst, Vic.	27·0	0·3	2·5	—	—	(0–1)	(1–4)	—	—	53·2
Mittagong, N.S.W.	24·7	0·3	3·1	—	—	(0–1)	(1–5)	—	—	48·0
Jericho, Qld.	25·7	0·1	3·2	—	—	(0–2)	(1–6)	—	—	49·6
Adelaide Hills, S.A.	27·2	0·1	2·1	—	—	(0–1)	(1–3)	—	—	51·2
$2n = 50$										
Barossa Valley, S.A.	37·2	0·3	3·5	3·8	—	(0–2)	(1–4)	(1–4)	—	—
$2n = 60$										
Myponga, S.A.	42·0	*	*	*	*	(0–3)	(1–6)	(0–2)	(0–3)	56·8

*Insufficient cells analysed to give data.

as well as the occurrence of chromosome unbalance. It is perhaps significant that the two plants in which neocentric activity has been detected come from areas close to one another in the Barossa Valley of South Australia.

IV. The Distribution of the Members of the Polyploid Series

The detailed distribution of the members of the polyploid series is shown in Figures 1 and 2.

The diploid chromosome number is found in populations on the slopes and tablelands of the Eastern Highlands of New South Wales, round through central and southern Victoria, and just into south-eastern South Australia. This diploid chromosome number is the only one found in Tasmania.

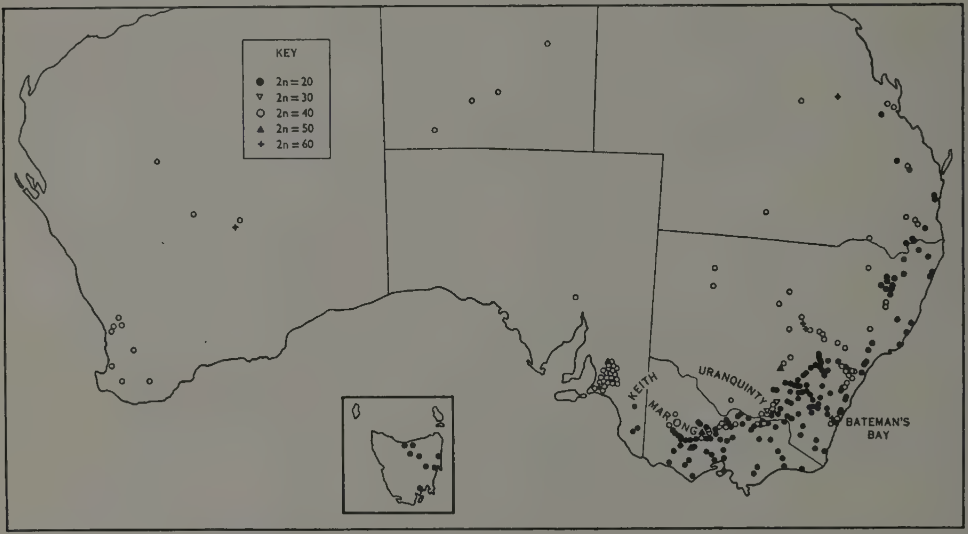

Fig. 1.—The distribution of the chromosome races of *Themeda australis* in Australia below the Tropic of Capricorn.

The tetraploid chromosome number is found in populations which lie inland with respect to the diploids, except for three small pockets on the eastern coastline—one near Sydney, one at Bateman's Bay in New South Wales, and perhaps one other near Rockhampton in Queensland. It is the only race in southern Western Australia, and the Mt. Lofty and Flinders Ranges of South Australia.

Triploid individuals have been found in two populations at the margin of the diploid and tetraploid races near Uranquinty in southern New South Wales. In one of these populations, both triploids and aneuploids with chromosome numbers between the diploid and triploid, i.e. $2n = 21$, 22, 23, 25, were identified. The aneuploids probably arose from crossing between diploids and triploids.

The pentaploid chromosome number has been found four times in individual plants from widely separate populations—from the Barossa Valley in South Australia, Beaufort and Marong in Victoria, and Wyalong in New South Wales.

The hexaploid chromosome number has been found five times, also in single plants from widely separate populations—at Laverton in Western Australia, at Myponga in the Adelaide Hills, at Trangie and Bateman's Bay in New South Wales, and at Fernlea in Queensland.

Collections which were made in the Adelaide Hills in an attempt to find diploid populations were sufficiently extensive for the failure to find diploids to be good evidence that they are absent from this region. For similar reasons, I believe tetraploids are not present in Tasmania.

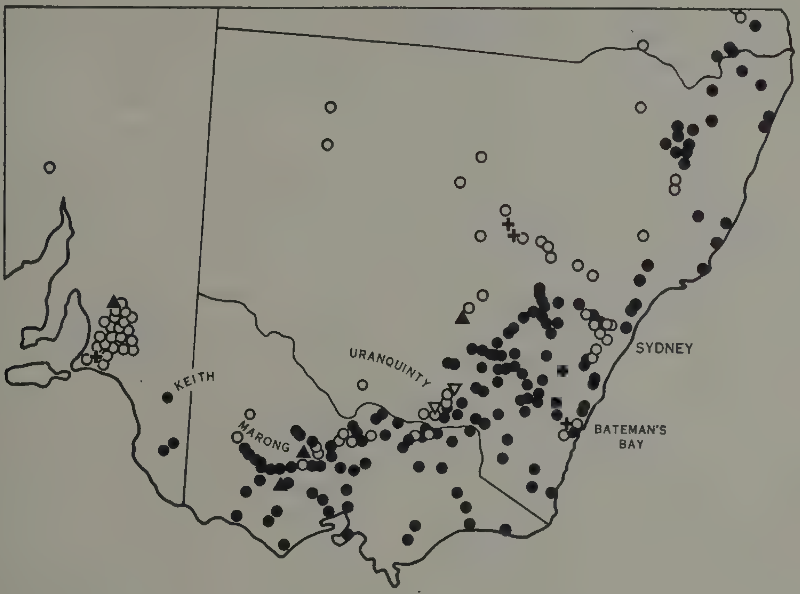

Fig. 2.—An enlargement of the south-eastern Australian portion of Fig. 1 to show detail. The key to the symbols is unchanged.

V. Discussion

(a) *Relationship between the Chromosome Races*

The formation of multivalent associations in the polyploids indicates a close degree of homology between the constituent genomes, and suggests possible bases for the evolution of the polyploids from the diploids.

The location of the triploid plants and their intermediate chromosome number argues for their origin by hybridization between a diploid and a tetraploid. The frequency of trivalent associations is very high and indicates very close homology.

Similarly, the pentaploid is of hybrid origin, the parents here probably being a tetraploid and a hexaploid. It is known that hexaploid plants occur in the Adelaide Hills near the location of one of the pentaploids, and other hexaploid plants or populations must be presumed to occur in the other areas where pentaploids have been found.

Hexaploid plants are always found in association with tetraploid plants, but not necessarily with diploid plants. If the presence of pentaploids is taken as evidence for the presence of hexaploids, there are five areas where the hexaploid occurs which are all remote from any present day diploid, and three areas where the diploid, tetraploid, and hexaploid races occur together. There are two different, probably alternative, modes of origin of the hexaploid. It may have arisen as the result of the spontaneous doubling of the chromosomes of a triploid hybrid; or as the result of the fertilization of an unreduced egg in a tetraploid by a normal diploid male gamete. The cytological evidence, although showing that there is some homology between all three genomes in the hexaploid, cannot distinguish between these alternatives. It might be argued that the absence of the diploid populations from an area occupied by the hexaploid would favour the second mode of origin. However, it is possible that a diploid ecotype was present at one time in these areas, even though no trace of it has been found during this study.

The average frequency of multivalents in the tetraploids is lower than in the triploids or pentaploids, but there may be as many as six in occasional cells. The simplest hypothesis to explain the origin of the tetraploid from the diploid involves direct autopolyploidy. This, however, is a rare process in plant evolution (Stebbins 1950). Furthermore it is difficult to distinguish with certainty between the products of direct autopolyploidy, and the products of evolutionary processes which involve hybridization between plants with varying degrees of genetic and chromosomal homology, and the occurrence of polyploidy before or after hybridization. In its extreme form, this latter situation approximates to segmental allopolyploidy (Stebbins 1950; Stebbins and Vaarama 1954).

It is of great importance to an understanding of this complex species if it can be shown that the diploid and tetraploid races can still interbreed, and that gene exchange is possible between them. The naturally occurring triploid hybrids, and the aneuploid hybrid swarm found near Uranquinty, suggest that this is so. Further, triploid plants from this area have been grown in the field surrounded by both diploid and tetraploid plants. The chromosome numbers of the progeny obtained by open pollination range from $2n = 23$ to $2n = 38$, suggesting possible hybridization with the diploid and tetraploid as well as self-fertilization.

There is no information at present about the consequence of hybridization between and among disjunct diploid and tetraploid populations.

(b) *Significance of the Distribution Pattern*

There is a clearly marked pattern in the distribution of the diploid and tetraploid races of *T. australis*.

Stebbins (1950) has emphasized that deductions about polyploidy and plant distribution are only valid where the polyploids are believed to be derived from the diploid species with which they are compared. It has been shown that this condition is properly fulfilled in the comparison between the diploid and tetraploid races of *T. australis*.

The distribution of the other species of the genus *Themeda*, as well as the distribution of the family Andropogoneae (Hartley 1958), strongly support the view that *T. australis* entered Australia from the north, and probably through Cape York. The diploid race, which must have been an original colonizer, was able to migrate southwards along the east coast of Australia into Tasmania. This involves movement from a tropical environment into a temperate one. Even though the diploid race is apparently unable to spread westward, it is able to succeed in a very wide range of habitats. This adaptability is also evident in the tetraploid race, which has spread southwards almost as far as the diploid race, and has been capable of further extensive migration throughout Australia to the west.

The difference in adaptability between the diploid and tetraploid races operates over an enormous range of environments from Queensland to Victoria. It is difficult, and almost certainly erroneous, to relate this difference to any one factor in the environment. The extent of the area makes it probable that a complex of environmental features is concerned, and that this complex is different for different regions.

The constant differential which exists over this area is that of chromosome number. Polyploidy may play a twin role in its genetic effect. It may result simply in a doubling of the chromosome number, usually with consequent results on the physiological properties of the plant; further, it may also restore fertility to an otherwise sterile chromosome combination, and therefore permit the incorporation of widely diverse genetic material in one organism. It is possible to suggest the genetic role of polyploidy in *T. australis*.

Because true autopolyploidy is so rare in plant evolution (Stebbins 1950), it may be argued that the tetraploid race evolved from a hybrid between two differing diploid ecotypes, and therefore brought together genetic variation which permitted the dispersal of the tetraploid race of *T. australis* into areas not within the potential of the diploid. If the diploid hybrid was sterile, the polyploidy need only have played the role of restoring fertility and permitting recombination. If the diploid hybrid was fertile, however, recombination and introgression could have taken place at the diploid level. Under these conditions, one would expect to find a diploid race colonizing the areas now occupied by the tetraploid. The fertility of the triploid hybrid found near Uranquinty suggests that the original diploid was not sterile, and shows that the doubling of the chromosome number alone, has an important role in the distribution of the species.

It cannot be maintained that the doubling of the chromosome number is the sole factor in determining the geographical difference between the diploid and tetraploid races; both the effects of polyploidy and recombination between different ecotypes would be concerned. Genetic variation need not come only from the postulated formation of the diploid hybrid. It is very likely that the tetraploid race of *T. australis* arose more than once. Evidence to support this may be found in the occurrence of two populations of the tetraploid race which appear to be separate from one another, and from the general area occupied by the tetraploid race. The first of these is the populations of tetraploids about Sydney. These are separated from the next tetraploid population by more than 100 miles across the Eastern Highlands, an area colonized by the diploid race, and one which must have acted as a geographical barrier for a very long time. The second disjunct population is at Bateman's Bay on the south coast of New South Wales. In both areas, however, it is possible that the tetraploid race was introduced after colonization of the area by man. Irrespective of the merits of these two populations as examples of the independent origin of tetraploid populations, the occurrence of tetraploid populations derived from different diploid progenitors would permit opportunities for hybridization and recombination at the tetraploid level. It is also probable that the effects of the doubling of the chromosome number are genotype-dependent, conferring further flexibility on the genetic system.

One of the most striking features of the distribution pattern of the two races is their exclusiveness. The intensity of collection is very high, and yet the area occupied by the diploids has no tetraploid populations in it, and so far as the information available shows, diploid individuals are absent from the inland, tetraploid-dominant areas. Although the same processes of hybridization and polyploidy must have occurred all over the area occupied by the diploid, there is no evidence of them in the populations counted. Again, one must accept the hypothesis that the physiological effects of polyploidy confer a selective disadvantage in the diploid area.

It has been shown that hexaploid plants of *T. australis* occur rarely, and then only as individual plants in populations of another chromosome number. The advantage conferred by polyploidy in tetraploid individuals is greatly reduced therefore at higher levels of polyploidy. Thus the concept of an optimum level of polyploidy (Stebbins 1950) is supported by these data from *T. australis*.

It is unsatisfactory, but at the moment inevitable, that the nature of the physiological effects of polyploidy which affect the distribution of the chromosome races of *T. australis* should be unknown.

It would not be surprising if a pattern, similar to that found in the distribution of the polyploid races of *T. australis*, was present in the distribution of the polyploid races of other widespread species of the native flora. Two major features may be identified in southern Australia as likely to contribute to the nature of the distribution pattern, by acting as discriminant sieves for the migration of different polyploid races. These are: the complex and changing environmental transect encountered in any migration to the west of the Eastern Highlands; and the past and present aridity in the area between Western Australia and South Australia, and South Australia and Victoria. Evidence suggestive of a distribution pattern in the polyploid races across southern Australia has been found in *Dianella* spp. and *Pultenea* spp. (Curtis 1952), and *Goodenia* spp. (Martin, unpublished data). Intensive studies of these, and of the other examples which exist, would increase the knowledge of the migration patterns and the evolution of our native flora.

There are several points of particular interest in the pattern of distribution of the two chromosome races of *T. australis* which may apply in similar studies of other species. The absence of the diploid race of *T. australis* from the Adelaide Hills is an unusual example of the disjunction between the flora of the Adelaide Hills and that of south-western Victoria. There is a very close relationship between the flora of the two areas, and it is reasonable to suppose that had the diploid race ever reached the Adelaide Hills in some previous climatic period it would still be present there today. Wood and Crocker (1947) have produced evidence that these two areas have acted as refugia during one or more recent cycles of great aridity. The evidence from the distribution of the two races of *T. australis* suggests that the environment between these two areas has been such that it has permitted discrimination against the migration of the diploid race for a very long period of time. It is unlikely that this barrier to migration is the one to which Wood and Crocker refer.

There is some evidence from the distribution of the races which indicates the length of time the diploid has been in Victoria. Only diploid races have been found in Tasmania. *T. australis* probably entered Tasmania at a time when there was a land connection between southern Victoria and Tasmania. The diploid race of *T. australis* must have been present in southern Victoria then, as it is now.

It is known that inland forms of both plant and animal species frequently spread eastward through the Hunter Valley (White and Key 1957). The presence of the tetraploid form of *T. australis* in this area appears to be a further illustration of this.

The cytological relationships between *T. australis* and the other species in the genus are not known. Strong taxonomic affinities exist between *T. australis* and *T. triandra* Forsk., the two species having been considered identical at one time (Black 1948). *T. triandra* is widely distributed, extending from South Africa to eastern Asia, and has been shown by Gluckman (1951) to be a polyploid complex with the same series of chromosome numbers as in *T. australis*. Gluckman studied 22 populations of *T. triandra* from South Africa. She found that the tetraploids occurred in low-lying frost-free country with high summer temperatures, the pentaploids and hexaploids were found at high altitudes with severe frosts and moderate summer temperatures, and the diploids in a diversity of climatic conditions. While the same evolutionary emphasis on polyploidy is evident in *T. triandra* as is present in *T. australis*, the pattern of distribution in the populations examined does not appear as clear as that which exists in *T. australis*.

VI. Acknowledgments

It is impossible to acknowledge individually all those people whose collections of seed have been used in this study. I am particularly grateful to Dr. and Mrs. F. H. W. Morley, Miss Nancy Burbidge, Mr. R. N. Oram, Mr. M. Gray, and Mr. T. Pickard of the Division of Plant Industry, C.S.I.R.O.; to Mr. L. J. Chinnick of the Division of Entomology, C.S.I.R.O.; to Mr. Cameron and officers of the New South Wales Soil Conservation Service; to Mr. Parsons and officers of the Victorian Lands Department; and to Mr. Marriot and officers of the Queensland Department of Agriculture and Stock.

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Explanation of Plates 1 and 2

Plate 1

Fig. 1.—Metaphase I. Meiosis in a diploid plant of *T. australis* from Omeo in Victoria. ×600.

Fig. 2.—Metaphase I. Meiosis in a triploid plant of *T. australis* from Uranquinty in New South Wales. Note the larger chromosome size and the eight trivalents. ×600.

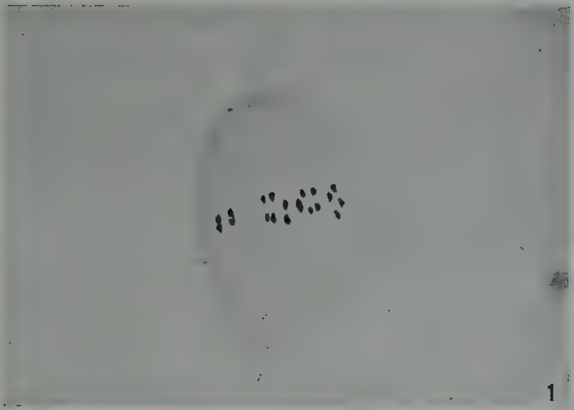
Fig. 3.—Metaphase I. Meiosis in a tetraploid plant of *T. australis* from the Barossa Valley in South Australia. These are two quadrivalent associations. ×600.

Plate 2

Fig. 1.—Metaphase I in a pentaploid plant of *T. australis* from the Barossa Valley. There are two clear quinquivalent associations. ×900.

Fig. 2.—Anaphase I. Neocentric activity present in the univalents of a pentaploid plant from the Barossa Valley. The univalents concerned lie axially in the cell, the ends or distal regions of the chromatids are directed towards the poles. ×900.

CHROMOSOME RACES OF THEMEDA AUSTRALIS



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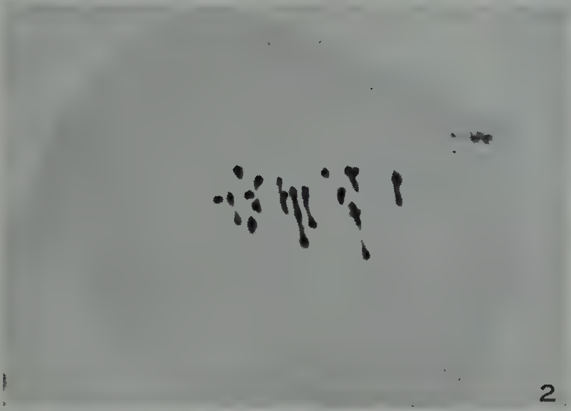

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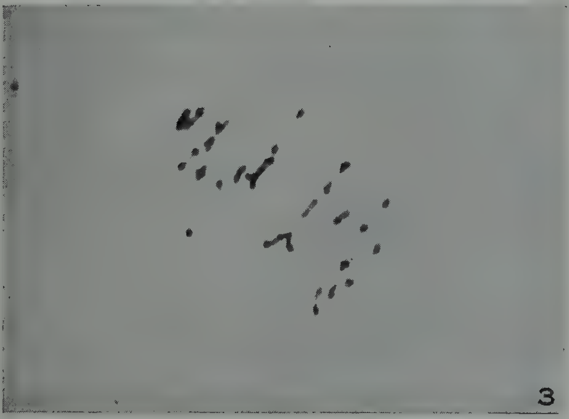

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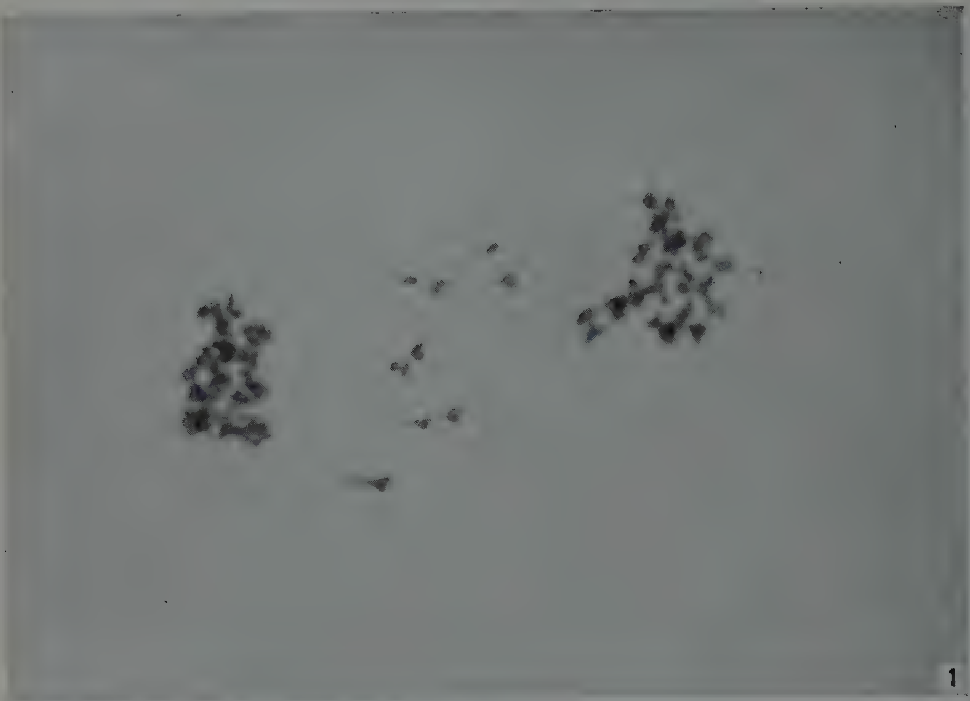

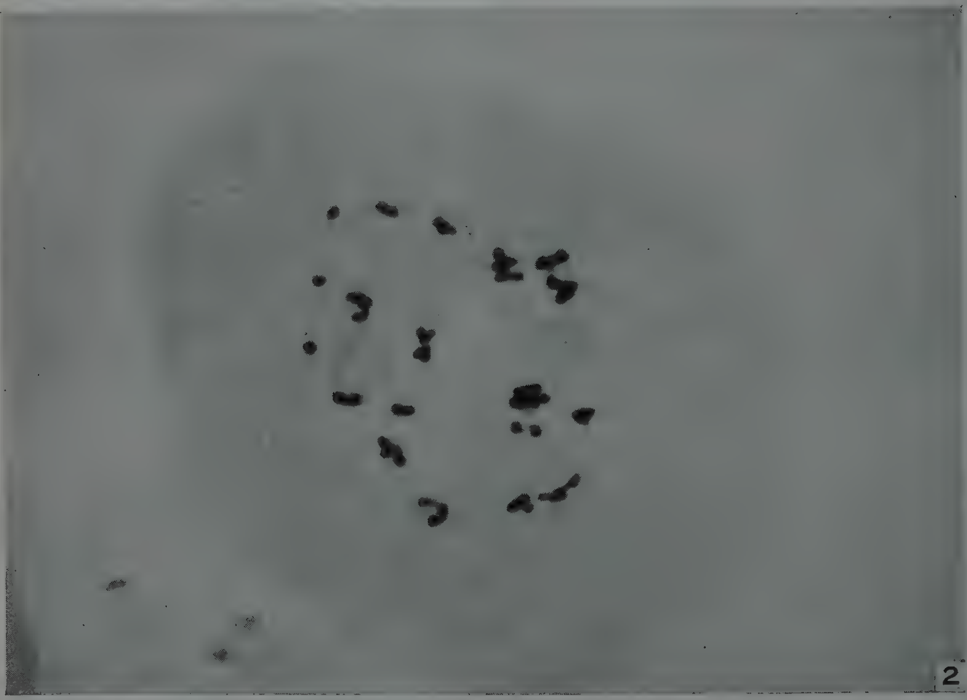

HOOK-SHAPED OPAL PHYTOLITHS IN THE EPIDERMAL CELLS OF OATS

By G. Baker*

[*Manuscript received August* 7, 1959]

Summary

Among several species of the Gramineae, *Avena sativa* L. (oats) is an important opal-accumulator plant in Victoria. In it, amorphous silica has been precipitated as very abundant microscopic opal phytoliths of various shapes, among which hook-shaped forms are common in alternating rows of epidermal cells. Examples studied in detail were observed within and isolated from oats grown on basaltic soil on "Barewood Farm", approximately 2 miles north of Clarkefield in the Romsey district of South Central Victoria. They are variable in shape and size, and in their relationships to adjacent rod-like opal phytoliths that infill the lumen of several of the subepidermal cells. Each hook-shaped opal phytolith consists typically of a solid core of opal enveloped distally by a more delicate cone-like sheath of opal. The opal of the sheath is hyaline and transparent compared with the thicker, generally translucent core.

Refractive index variations reveal differences between core and sheath, and between the several growth layers of slightly different composition in the sheath. These differences reflect variable ratios of silica to water in the opal of the core, the sheath, and its several layers. The hook-shaped opal phytoliths, like all other shape types secreted in short-lived plants, must have developed rapidly, because processes of opal precipitation and solidification were completed within the compass of one growth season.

I. Introduction

Hook-shaped opal phytoliths are well developed in dried-out silica-accumulator species of the grass tribe cut at the end of a season's growth. In the species of oats examined from the Clarkefield district of South Central Victoria, the processes of secretion and deposition of inorganic substances had ceased and the silica was precipitated in the solid amorphous state, the silica having been obtained by the plants from basaltic soils. As a result, a large number of opal phytoliths of several different shapes were formed, among which hook-shaped varieties are notable. These were readily isolated for examination in Canada balsam mounts and in refractive index liquids to determine their shape, size, growth structures, and optical properties.

The basaltic soil on which the oats were grown is a black, fine-textured clay which is somewhat plastic when wet, friable when dry, and rich in humus; tests of the top 6 in. by electrometric means revealed that the soil has a pH value of 5·2. At a depth of 11 in., the black topsoil changes into a greyish brown clay.

The clay fraction constitutes the greater part of the black topsoil, and this is accompanied by a small proportion of coarse and fine sand fractions constituted of occasional pellets of limonite, granules of partially altered basalt, grains of augite, plagioclase, olivine, iddingsite, leucoxene, and opaque iron oxides from the basalt, opal phytoliths (mainly rod-like forms) from plants, and a few grains of quartz ranging up to 1 mm in size. The quartz was evidently washed or blown into the soil from

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*Mineragraphic Investigations Section, C.S.I.R.O., University of Melbourne.

adjacent weathered outcrops of Silurian sandstone which in places is transected by veins of reef quartz. Elsewhere, the Silurian is covered by the flows of Newer Basalt from which the soils were largely derived.

The average rainfall in the district is 28 in. per annum.

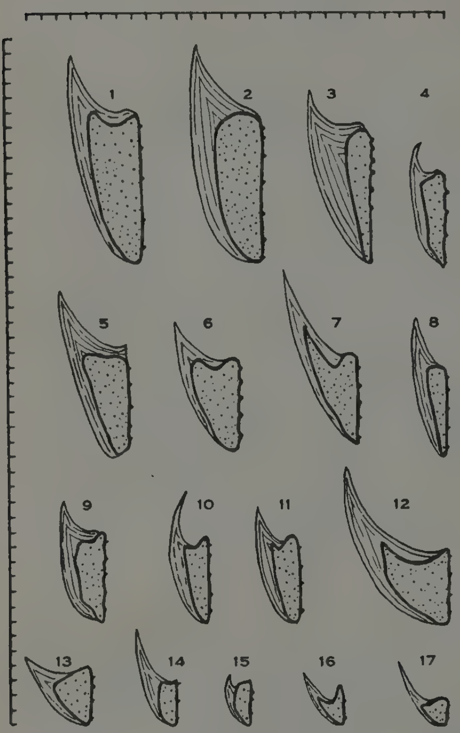

Fig. 1

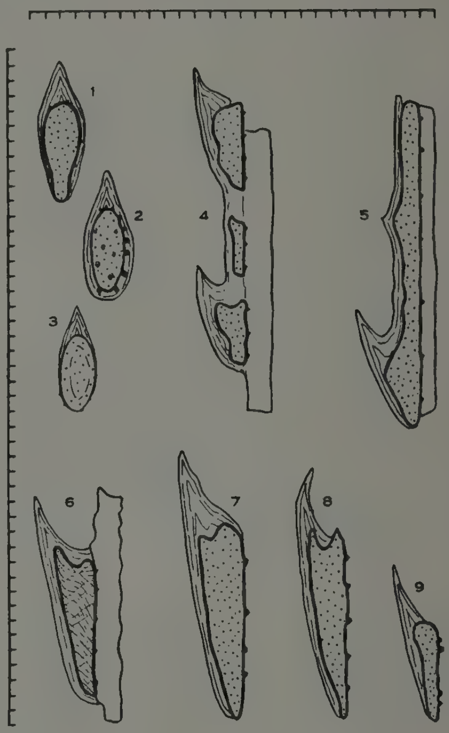

Fig. 2

Figs. 1 and 2.—Sketch diagrams of hook-shaped opal phytoliths from the epidermal cells of oats, showing size and shape variations. Stippled areas represent solid cores with small spinose outgrowths ("anchors"); lined areas represent sheaths with growth layers. The hooks are depicted in the positions they occupy in an erect stem or flower stalk. Each scale graduation represents 0·010 mm.

In Fig. 2, Nos. 1–3 represent basal aspects (i.e. views of proximal surfaces) of individual hooks; Nos. 4–6 show complex hooks "welded" to rod-shaped opal phytoliths; Nos. 7–9 show single hooks. The core of Fig. 2, No. 6, shows a delicate growth-line pattern.

II. Size, Shape, and Growth Structures

The hook-shaped opal phytoliths vary from approximately 20 to 180 μ in length, from 30 to 75 μ in depth, and from 20 to 30 μ in width. The variation in size is evidently due to differences in the amounts of siliceous solutions supplied to the sites of opal precipitation.

Shape variations accompany differences in size. Typical examples are illustrated in Figures 1 and 2, in addition to which there are further minor variations.

The characteristic features of the hook-shaped opal phytoliths are: (*a*) an inner core of translucent opal, surmounted by (*b*) an outer layered sheath of crystal clear opal. As observed *in situ* in the host plant, the opaline core regions occur embedded in the epidermal cells, while the greater part of the sheath projects beyond the external surface of the plant. Comparable examples occur, more especially on the flower stalks, on some species of *Poa* in Victoria, and also on other members of the grass tribe that are harsh to the touch.

The ultimate general shape of each hook is largely determined by that of the initially precipitated core, as evidenced from inspection of Figures 1 and 2, but the final outline of the hook does not invariably conform exactly with that of the inner core in all its details.

Several of the cores are crudely heart-shaped in side aspect (Fig. 1, Nos. 1, 10, 11, and 16; Fig. 2, Nos. 6 and 7); some are club-shaped (Fig. 2, No. 9) or baton-shaped (Fig. 1, No. 8); others are triangular in outline (Fig. 1, No. 13) or bun-shaped (Fig. 1, Nos. 2 and 15); the remainder have nondescript shapes.

The majority of the cores are elongated in one direction according to the dimensions of the containing epidermal cells. The sheath opal never extends around to nor over the proximal surface of the core, but is built up in layers above its distal surface in the form of a cone. The cores do not reveal definite layering effects like the sheaths, although rare examples (Fig. 2, No. 6) show a complex pattern of fine criss-cross lines that evidently represent growth lines. Even though every core does not necessarily have a prominent apex as in Figure 1, Nos. 1, 6, 7, 10–12, 16, and 17, the sheath always forms a peak at the distal end of the cone-shaped structure. This apex is often sharply pointed (Fig. 1, Nos. 1–17), but can be rounded and rather blunt (Fig. 2, No. 8); this means that hooks observed in soils or dusts to possess rounded apices have not all necessarily been modified by slight abrasion or chemical corrosion after release from the host plant. The sheaths of the hooks protrude outwards and upwards (cf. Figs. 1 and 2) from the epidermal cells, although some recurve inwards towards the surface of the plant (Fig. 1, Nos. 4, 10, and 15; Fig. 2, No. 8).

A variable number (6 to 18) of small spinose outgrowths (Figs. 1 and 2) from the cores serve to anchor the hooks by their proximal surfaces to cell wall linings (cf. Baker 1959*c*) of opal in some epidermal cells, or to replaced cell walls. Areas of the proximal surfaces between the spinose outgrowths are usually smooth and flat, but some reveal small crenulations (Fig. 1, No. 9; Fig. 2, No. 4) that conform to the wavy configuration of the inner walls of the epidermal cells.

Plan aspects of the proximal surfaces of the cores generally reveal an oval outline (Fig. 2, No. 3) around which the base of each sheath appears as an encircling girdle. Sometimes the outline of the core is crudely pear-shaped (Fig. 2, No. 1). When the number of spinose outgrowths is greater than usual, the core has a more irregular outline (Fig. 2, No. 2) and appears ragged, but this does not affect the sheath, which remains smooth and even in outline.

The growth of the cores is sometimes contiguous from one epidermal cell to the next, resulting in an elongated core of irregular shape in side aspect. Subsequent growth of the sheath layers extends along and over this structure to produce more complex types of hook structures, in which a well-developed hook is formed over the thickest parts of the core, an incipient spine-like growth is built up over less prominently elevated portions of the core, and a thinner covering film of even thickness is deposited over the thinnest parts of the core (e.g. as in Fig. 2, No. 5). Further complexities arise where the proximal surfaces of some cores become firmly attached by "welding" onto opal-replaced cell walls, which, in turn, are "welded" to underlying rod-shaped opal phytoliths produced by infilling with amorphous silica of the lumen of the cells in the layer beneath that containing the cores of the hooks (e.g. Fig. 2, Nos. 4–6). In this way, several hooks, replaced cell walls, and rod-shaped opal phytoliths become linked together, thus reflecting more advanced phases of autosilicification. One complex piece observed intact was 2 mm long and 0·100 mm wide, with seven hooks "welded" together in a row and attached to opalized cell walls and rod-shaped opal phytoliths.

III. Optical Properties

Hook-shaped opal phytoliths teased out from their plant host, and examined in Canada balsam mounts under crossed nicols of a petrological research microscope, are all observed to be completely isotropic. As seen *in situ* in the host plant, however, the outer edges of some of the hyaline sheaths show apparent birefringence when in proximity to strongly birefringent cellulose portions of the plant tissues; the bulk of each hook remains isotropic.

None of the opal phytoliths fluoresced under a "Mineralight" ultraviolet lamp.

Most of the opal phytoliths are colourless in ordinary transmitted light, with the larger, thicker examples frequently showing a very faint pinkish tinge which probably results from slight dispersion of transmitted light under the microscope, rather than from any particular trace element in the opal. A few of the cores of the hooks have a pale milky appearance, but the strongly coloured (brownish) to opaque varieties recorded from soils (Baker 1959*a*, 1959*b*) and dusts (Baker 1960) are not represented.

Refractive index variations, observed in Canada balsam mounts of the hook-shaped opal phytoliths, are evident from Becke line effects at junctions between various layers of the sheaths, and between cores and sheaths. Determinations in refractive index liquids by the immersion method reveal an overall range from $n_{Na} = 1 \cdot 430$ ($\pm 0 \cdot 001$) to $n_{Na} = 1 \cdot 452$ ($\pm 0 \cdot 001$) in the opal of all shape types of opal phytoliths present in the oats examined. The range is more restricted within the group of the hook-shaped forms, the component parts of which show a range in n_{Na} from $1 \cdot 434$ ($\pm 0 \cdot 001$) to $1 \cdot 440$ ($\pm 0 \cdot 001$) for the sheaths, and from $1 \cdot 438$ ($\pm 0 \cdot 001$) to $1 \cdot 442$ ($\pm 0 \cdot 001$) for the cores. By contrast, among the other shape types of opal phytoliths represented, the common rod-shaped and needle-like varieties range from $n_{Na} = 1 \cdot 436$ ($\pm 0 \cdot 001$) to $1 \cdot 452$ ($\pm 0 \cdot 001$), with the majority occurring between $1 \cdot 438$ and $1 \cdot 450$. Hat-shaped forms are commonly in the upper range of $n_{Na} = 1 \cdot 450$ ($\pm 0 \cdot 001$) to $1 \cdot 452$ ($\pm 0 \cdot 001$), while thin plates broken from cell wall linings are in the lower range of $n_{Na} = 1 \cdot 430$ ($\pm 0 \cdot 001$) to $1 \cdot 436$ ($\pm 0 \cdot 001$).

The refractive index of opal decreases as the water content increases. Over the range 8·97 to 3·55 per cent. water, the variation in refractive index is linear, from 1·446 to 1·460 (Winchell 1951). Extrapolating to cover the range 1·430 to 1·446, it is apparent that the water content of the opal phytoliths under discussion ranges from 6·5 to 14·5 per cent. The general range in the hooks is from 11·3 to 13·0 per cent. water, and the difference between any one core and its attached sheath is approximately 1 to 1·25 per cent. of water, with more in the sheath opal than in the core opal.

IV. EFFECTS ON HOOK-SHAPED OPAL PHYTOLITHS AFTER RELEASE

On being shed from the opal-accumulator plants in which they were generated, following the withering of the plant and decomposition of the organic matter, the two main structures of the hook-shaped opal phytoliths, i.e. the core and the sheath, normally become separated fairly rapidly. Being resistant and more solid, the cores are more persistent as constituents of soils and dusts, but their small spinose outgrowths do not remain attached for long, and are often only evident as short, curtailed stumps. Several of the opal phytoliths described as having oval- and pear-shaped outlines among the assemblages of different shape types in soils and dusts (Baker 1959*a*, 1959*b*, 1960), are obviously the cores of hooks from which all traces of the sheaths have disappeared.

The fragile, thinner sheath structures are seldom observed in soils or dusts, whether still attached to, or as separate entities detached from, the cores. The relative ease with which some sheaths become separated from their cores has been noted when teasing out the hook-shaped opal phytoliths from the dried host plant for microscope preparations. The sheaths sometimes become detached whole and in the form of asymmetrical hollow cones; a few of the thinner, more delicate sheaths become shattered to fragments. These thin-walled, hollow cones do not survive as complete entities for long, once decomposition of the host plant commences, nor when subjected to rubbing and grinding between the molar teeth of ruminant animals. As observed in the faeces of sheep (and rather less so in the faeces of rabbits), many cores of the hooks have withstood the crushing processes of the teeth, but virtually all of the sheaths have been fractured into thin fragments.

Furthermore, the thin sheaths of the hook-shaped opal phytoliths are more easily fused than the solid cores. On mounting a concentrate of opal phytoliths from oats in acrylic resin in a mould subjected to pressures of up to 1 ton and temperatures of up to 180°C for 15 minutes' duration, differential fusion of the opal occurred. Microscopical examination of the cooled product revealed that the only non-fused remnant opal phytoliths were solid rod-shaped forms and the resistant cores of hook-shaped forms. The thinner cell wall lining types of opal phytoliths, the thinner sheaths of hook-shaped forms, and the smaller hat-shaped, boat-shaped, and needle-like examples were all fused into spheroidal aggregates of dehydrated opal (forming a silica glass). It seems likely that these thin and smallest opal phytoliths might become partially fused on release from opal-accumulator plants during grass fires; they are most certainly readily fused under the conditions of haystack fires.

V. CONCLUSIONS

Hook-shaped opal phytoliths composed of thicker cores and thinner, layered outer sheaths are characteristic forms of the outer parts of such opal-accumulator plants as certain species of *Avena*, *Poa*, and other allied genera of the Gramineae in Victoria. They occur in some rows of the epidermal cells, separated by other rows that are free of opal phytoliths. Those examined from oats grown on basaltic soil at Clarkefield in South Central Victoria reveal that the more solid cores were secreted first in firmly embedded positions in the epidermal cells. Later-secreted opal that developed into cone-like sheaths enveloping the distal portions of the cores was precipitated in layered growth structures. Refractive index differences between these layers reflect a varying water content within each sheath, but comparable variations are not evident within each core. Refractive index variations also reflect differences in the water content of cores and sheaths generally. Apparently the cores were precipitated when a steady supply of siliceous solutions was available, thus giving each core uniformity of composition. The sheaths, on the other hand, were built up in stages, evidently during the end phases of the life of the accumulator plant. The variations point to: (i) intraseasonal periodicity effects arising from changes in such factors as rainfall, evaporation, etc. that affect supplies of solutions to the plant from the soil, or else (ii) some specific control of opal precipitation that operates more dominantly just prior to the completion of the growth season, at which time most of the opal seems to be deposited within an opal-accumulator plant.

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The oat plants examined for their opal phytolith content, the samples of the basaltic soil on which the oats were grown, and rock specimens representative of the locality were collected by the author from "Barewood Farm", near Clarkefield, through the courtesy of the owner, Mr. E. Hope.

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THE PHYTOGEOGRAPHY OF THE AUSTRALIAN REGION

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Summary

The Australian phytogeographic region is defined as including the Australian mainland and Tasmania. This region may be subdivided into the Tropical Zone in the north and east, the Temperate Zone in the south and east, and the Eremaean Zone in the arid centre. Delineation of these zones is closely linked with present-day climates but their floristic constituents also reflect selection resulting from past climatic and geographic conditions. The following areas are of special phytogeographic interest: South-West Province of Western Australia, Tasmania, North-East Queensland, and the MacPherson–Macleay Overlap where the Tropical and Temperate Zones coincide. Three interzone areas have been defined where special circumstances prevent the drawing of zonal boundaries.

In Parts A and B floristic analyses covering the distribution of Australian phanerogamic genera are provided for the Australian Region and for the special areas listed above. The analyses deal with family representation, endemism, and the estimated number of species present.

The flora of the South-West Province reveals the highest proportion of endemism though there is a close relationship with the flora of the eastern part of

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the Temperate Zone. The existing west–east affinities and discontinuities are discussed in relation to climatic changes. The Province is not regarded as the "cradle" of the autochthonous elements of the Australian flora though it is apparently an asylum for many relict forms. Affinities with the flora of South Africa are not higher than those for other areas of the Australian Region.

The flora of Tasmania is not highly endemic at the generic level but it is of special interest because of certain affinities with the flora of Malaysia and with genera otherwise found along the Malaysia–New Zealand arc or genera also in South America. In some cases the genera are unknown on the mainland, in others they are known from Australian Tertiary deposits. The Tasmanian flora is considered to include (1) relicts from early Tertiary floras, (2) survivors from the cold climate regimes of the Pleistocene, and (3) Australian elements which have mingled with the flora during periods of land continuity.

The North-East Queensland area is defined as including the high rainfall habitats of the eastern parts of Cape York Peninsula. An outstanding number of families, genera, and species are restricted to this area so far as the Australian Region is concerned. Many genera are limited to a single representative which may also occur in Malaysia. It is suggested that a proportion of these may be recent arrivals while others, known as fossils from southern deposits, have a more restricted distribution than in the past. The close affinity with the flora of New Guinea is obvious but there are certain affinities with the floras of New Caledonia and New Zealand which may be independent of those of other parts of the Australian Region. Consideration is given to the problems of migration of temperate elements between the northern and southern hemispheres and the passage of such elements through the tropical belt.

The MacPherson–Macleay Overlap is defined as that area of eastern Australia where the Tropical and Temperate Zones overlap. It includes part of south-east Queensland and part of north-east New South Wales. Within this area tropical elements predominate in the wetter habitats of the eastern slopes of the ranges and temperate elements in the drier or cooler and more open sites. Many of the tropical elements are to be found in discontinuous areas to the south of the Overlap but there is no similar pattern of temperate communities to the north. The Overlap is of special interest in the discussion of discontinuous distributions in eastern Australia and the significance of these.

The development of the Australian flora is discussed in Part C. Its present composition is regarded as primarily due to climatic selection both within the region and from the biotypes available as a result of migration. Migration by communities rather than by chance dispersal of individuals is considered a prime factor.

Though the data concerning Tertiary floras are not extensive certain significant facts emerge. First there is a stronger affinity with the flora of South America and this must be contrasted with the marked lack of data suggesting a similarly increased relationship with southern Africa. The relationship between fossil and modern representatives of such genera as *Podocarpus*, *Dacrydium*, and *Nothofagus* suggests that there has been a northward migration or a withdrawal to warmer latitudes since the Tertiary. All the main elements of the present day flora are represented in the Tertiary assemblages. If current views on the "Malaysian" or "tropical" nature of some affinities and the "Antarctic" nature of others be accepted then there is no indication that the major migration into the Australian Region came from one particular direction.

Possible climatic regimes and changes are discussed. It is suggested that the occurrence of cold pluvial conditions in southern Australia implies a contraction of the arid centre rather than a northward shift of the dry tropical belt. Under such circumstances northern Australia could still have enjoyed a warm wet climate.

This opinion is supported by certain distribution patterns and by the pedological data concerning laterite formation.

Apart from the Australian, Malaysian, and Antarctic elements in the Australian flora there are also temperate elements with northern hemisphere affinities. Some of these are found in temperate communities in both hemispheres but others are endemic to and characteristic of the Eremaean Zone. The Eremaean flora may have originated from a coastal sand dune and littoral type. It is suggested that it developed from elements that migrated to the Australian Region as early as the Cretaceous when there may have been a coastal continuity with the Tethys Sea. It is further postulated that these plants remained in coastal habitats but moved inland, possibly along southern estuarine coasts, and became isolated under arid conditions during the Pleistocene or Recent Times.

The evidence is that eastern Australia has been a very important migration route for a very long period, being linked with the northern hemisphere through Malaysia. Northward migration of Australian elements has apparently been less successful than southward migration of Malaysian elements. It is considered that the ecological barrier formed by dense tropical communities must have inhibited northward movement of the light-requiring Australian types. The significance of such a barrier would be dependent on the climatic conditions during periods of land continuity between Australia and Malaysia and between Australia and New Guinea.

Relationships between the Australian Region and New Zealand are either linked with those between Australia and South America, i.e. related to some unknown southern route, or they concern genera with distribution patterns involving New Guinea or New Guinea and New Caledonia. The opinion that Australia and New Zealand belong together in a biogeographic region is unacceptable unless such a region includes a portion of the island arc in the north-east.

The long-standing floristic relationship between Australia and Malaysia, a relationship which from geological evidence apparently extends back as far as the Cretaceous at least, coupled with the affinities among both fossil and modern plants with the flora of South America but not with southern Africa, militates against unqualified acceptance of any of the hypotheses, such as that of continental drift, which have been proposed to explain biological affinities between the major land masses. Plant distribution patterns are facts which can be demonstrated and at this stage of our knowledge further critical analysis is more important than the correlation between available facts and proposed explanations.

A. THE PRINCIPAL FLORISTIC REGIONS

I. INTRODUCTION

As discussed here the Australian floristic region is understood to consist of the Australian mainland and Tasmania. In the north-east there is a close association with the boundaries of the Malaysian Region which is taken to be that area considered by the collaborators in the new *Flora Malesiana*. This association is, at the present time, through New Guinea but some of the important results of the interactions which have occurred between the two regions and the effects these have had on the flora of the Australian Region will be discussed in various parts of the text below. Apart from this the relationships with other regions appear to have been at more remote periods in geological time and for this reason the number of genera which are also represented in other continental areas such as South

America or in now isolated islands such as Madagascar, New Caledonia, and New Zealand is of particular interest.

The Australian land mass has no topographical features of major importance, though the Dividing Ranges in eastern Australia form what appears to be a definite migration route, and consequently it is the climatic factors which to a large extent dictate the present delineation of the main floristic zones. There are no great river basins having their own special characteristics, no high mountains to bar the way to migrating communities, and the coastline is relatively unindented.

The continent is crossed from west to east by the Tropic of Capricorn and it is therefore markedly affected by the high pressure desert areas common in such a latitude. There are two main rainfall systems, that in the north being monsoonal and summer in its incidence while that of the south is winter in incidence and results from the passing of Antarctic low pressure systems.

Treated broadly the continent can be divided into three main climatic zones and these are referred to here as the Tropical, Temperate, and Eremaean Zones (see Fig. 1). The boundaries between these Zones are not always sharp, owing to differing tolerances of characteristic genera but it is hoped that the data presented will serve to justify their delineation as phytogeographic units. Each of the Zones shows floristic characteristics related to geography and it is interesting to find that they correspond with the main features of the zoogeographic "regions" recognized by Main, Lee, and Littlejohn (1958).

Tropical Zone.—This is a crescentic area with one point resting on the Western Australian coast in the vicinity of the Tropic and the other covering the extreme north-east corner of New South Wales and part of the coastal areas. In Western Australia it includes the North Province as defined by Gardner (1944), i.e. the Pilbara District and the Kimberley. From here it extends across the northern part of the Northern Territory to the north of Newcastle Waters, through the country around the Gulf of Carpentaria and down the east coast and subcoastal areas of Queensland. The New South Wales section is that referred to as "North Coast" by Anderson (1957), i.e. the eastern slopes of the ranges and the coastal forests in the northern section.

The zone is characterized by a dry monsoonal climate. Floristically it is rich in Malaysian elements as well as in Australian endemics. As described by Specht (1958) in his account of the flora of Arnhem Land the occurrence of some of the Malaysian elements is very discontinuous. Some of the most interesting representation is limited to the eastern high rainfall areas of the Cape York Peninsula and in the discussions below this is referred to as "North-East Queensland".

Temperate Zone.—Like the Tropical Zone this is crescentic in outline. It covers the south-west corner of Western Australia, South Australia within the 10-in. isohyet (i.e., receiving more than 10 in. rain per annum), Victoria (except for the north-west corner), Tasmania, and eastern New South Wales from the western slopes of the Dividing Range to the coast, and then narrows into the eastern point of the crescent so as to cover the eastern Darling Downs and the Dawson, Burnett, and Moreton Districts of south-east Queensland. It will be noted that the eastern points of the Tropical and Temperate Zones overlap. This area is defined here as the MacPherson–Macleay Overlap and within it the Tropical elements are usually found in the moister habitats of the gullies and on the upper parts of the eastern slopes of the ranges while the temperate elements are best developed on the more open habitats of the plains and tablelands. The main part of the Overlap lies in the area of the MacPherson Ranges in the north and the Macleay River in the south, though disjunct occurrences of some of the plant communities might dictate a southward if not a northward extension.

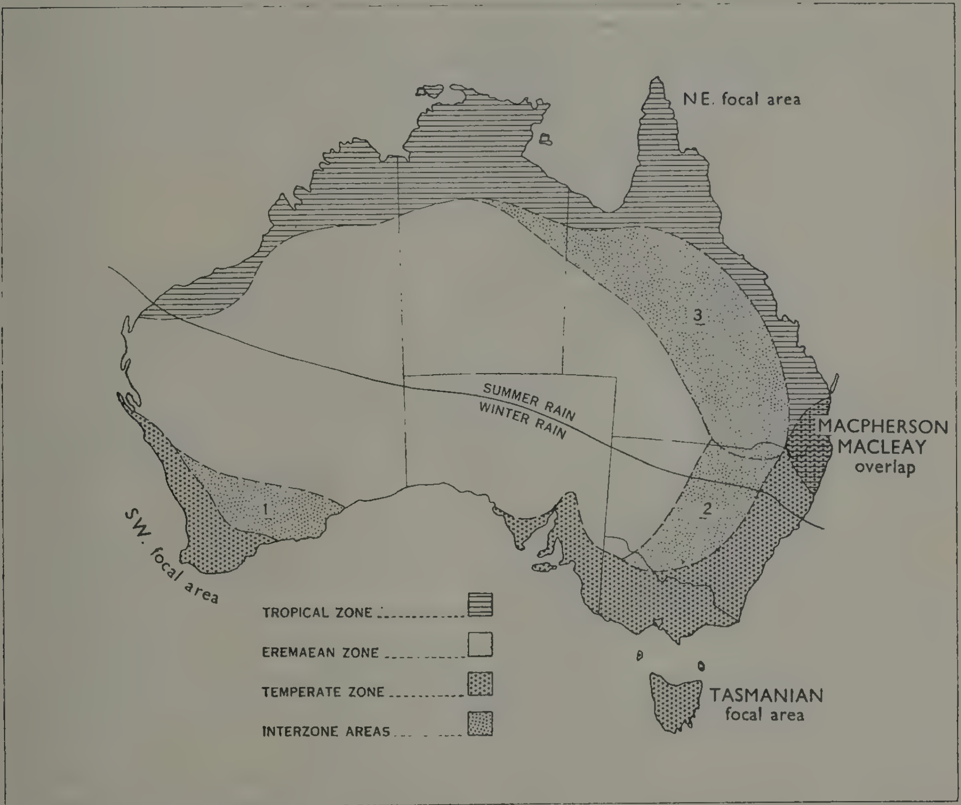
N.E. focal area
3
SUMMER RAIN
WINTER RAIN
MACPHERSON
MACLEAY
overlap
1
2
S.W. focal area
TROPICAL ZONE
EREMAEAN ZONE
TEMPERATE ZONE
INTERZONE AREAS
TASMANIAN
focal area

Fig. 1.—The principal floristic zones of the Australian Region.

The Temperate Zone has a cool to warm temperate or subtropical climate and precipitation is mainly winter in its incidence except in the eastern and south-eastern sections where it may be fairly evenly distributed throughout the year or may show both winter and summer maxima. Floristically the most interesting areas are the South-West Province of Western Australia as defined by Gardner (1944), Tasmania, and the MacPherson–Macleay Overlap.

Eremaean Zone.—This Zone is considered to cover the whole of arid Australia. The term was originally defined by Tate (1890) for a portion of northern

South Australia and was spelt "Eremia". It was redefined under the current spelling by Diels (1906) and was further discussed by Gardner (1944). It extends from the drier parts of the Western Australian coast around Shark's Bay to the Darling River in New South Wales. In the north it is bounded by the Tropical Zone but the south-western, eastern, and north-eastern limits are not as easily recognized. For this reason three interzones have been recognized and are defined below.

The climate of the Zone is characterized by the extreme variability of the rainfall both annually and seasonally. The Zone is crossed obliquely by the junction between the summer and winter rainfall systems but floristically the junction is not so strongly marked, and, furthermore, it is partially obscured in the analysis of data by the existence of a number of small ranges of low mountains, in Central Australia, which appear to have acted as refugia for both northern and southern elements. Apart from such refugia the gradation in the floristic composition from north to south is probably as closely related to temperature gradients and possibly also day length as to available rainfall.

Interzones.—In general the southern boundary of the Eremaea is based on the position of the 10-in. isohyet. However, in Western Australia there is a triangular area lying between the South-West Province and the Eremaea proper. The placing given this area has varied according to different authors. Within it there is some mingling of the genera of the sand heath associations of the Province with the aridity-tolerant genera of the Eremaea. To some extent this interrelationship is linked with local edaphic conditions but for the present it seems best to place the area in an intermediate position as Interzone 1. It has a dry climate with a rainfall mainly winter in incidence.

Interzone 2 covers much of the central parts of New South Wales, i.e. the Western Plains between the Darling River and the western slopes of the Tablelands (Anderson 1957). Floristically the area is markedly affected by the floodplain system of the upper Darling and Lachlan Rivers. Temperate genera follow the better-watered habitats but there is an increasing representation of Eremaean elements on the drier habitats as one moves from east to west. The Interzone is, therefore, a mosaic and no clear boundary can be drawn. The general character of the vegetation of the interzone is shown by Beadle's map (1948).

North of the Barwon River there is the boundary of the "black soil" system which covers much of Central Queensland and extends as far to the northwest as the Barkly Tableland of the Northern Territory. This area is defined as Interzone 3 and, like Interzone 2, the general representation is markedly affected by the intersecting river systems, not primarily because of the greater availability of water but because of edaphic differences and the presence of deep alluvium. Because of this effect of the water courses and the peculiar properties of the black soils a clear boundary cannot be drawn on the basis of current information. Relevant ecological studies have been published by Blake (1937) and by the Land Research and Regional Survey Division of C.S.I.R.O. following their survey of the Barkly Tableland (C.S.I.R.O. Aust. 1954).

II. General Analysis of the Phanerogamic Flora

The data on which this account is based concern the distribution patterns revealed by the occurrence of genera. Data on species distribution vary in accuracy and detail even though much may be learned by studying such an analysis as that of Specht (1958) based on the flora of Arnhem Land. Until such studies are available for other areas, especially in the absence of a modern reference flora for the Region, it is only possible to treat the flora in a broad sense at the family and generic levels.

All the phanerogamic genera recorded for Australia, apart from naturalized aliens, have been taken into account though in a few cases the taxonomic standing of the genus, the lack of information regarding its distribution, occurrence, or nomenclatural status is so unsatisfactory that it has been necessary to exclude them. It is believed that the main conclusions are not affected by these omissions.

Data regarding cryptogams are much less comprehensive and have therefore been omitted.

Apart from the gymnosperms, which are poorly represented in the Australian Region, the flora includes genera from 188 families (Englerian system plus recently described families). Since there has been no general account of the flora for many years it is inevitable that treatment of the different genera is not always consistent but under the present circumstances this seems unavoidable. In general where recent studies have involved changes in generic circumscriptions the smaller units have been accepted for this analysis. In no case has the use of a modern treatment meant a reduction of generic numbers. That some of the newer treatments do not seem altogether justified by field experience has been considered less important than the fact that such recognition of minor generic units probably indicates an evolutionary development which has reached a stage beyond that of the specific level. Cases in point where new treatments have been published but which have not yet been accepted into general use for the Australian flora are to be found in the Loranthaceae (Danser 1929), Chenopodiaceae (Ulbrich 1934), Cruciferae (Schulz 1936), Convolvulaceae (van Ooststroom 1938–52, Hoogland 1952–53) and to a lesser extent the changes resulting from the work of Sleumer in Proteaceae (1955), and Wimmer in the Campanulaceae (1943, 1953). Bremekamp's study of the Acanthaceae (1948) has left a number of Australian taxa without a proper generic position and they can only be dealt with tentatively.

In Table 1 below the flora is analysed according to generic representation within the various families. The numbers recorded for Australia–Tasmania, i.e. for the Australian Region, are compared with those of the world and some general remarks on distribution are also given. The data regarding world distribution and generic numbers are mainly based on those provided by Willis's Dictionary (1951) and are included so as to provide the reader with a scale, approximate though it must be, against which the relative importance of the Australian elements can be assessed. The Australia data have been collated by the present author in a "Dictionary of Australian Plant Genera" which is not yet published.

TABLE 1

GENERIC REPRESENTATION WITHIN FAMILIES

Temp, Temperate Zone; *Trop*, Tropical Zone; *Er*, Eremaean Zone; *MMO*, MacPherson–Macleay Overlap; *SWP*, South-West Province of Western Australia

Family	Total Genera (approx.)	World Distribution	Australia–Tasmania		Chief Distribution of Family in Australia–Tasmania
			Total Genera	Endemic Genera	
GYMNOSPERMS	50	Cold temperate to mts. in Tropics	14	9	1 widespread, others mainly E. Australia and Tas.
MONOCOTYLEDONS					
Typhaceae	1	Temperate and Tropic	1	—	General
Pandanaceae	3	Old World Tropics	2	—	N. and E. *Trop*
Sparganiaceae	1	N. Temperate and Australia	1	—	E. Australia
Potamogetonaceae	9	Cosmopolitan	7	1	Mainly coastal waters and *Temp*
Najadaceae	35 or 1*	Tropics and warm Temperate	1	—	*Trop*
Aponogetonaceae	1	Old World Tropics and S. Africa	1	—	*Trop*
Scheuchzeriaceae	5	Temperate	2	1	1 general, 1 endemic *MMO*
Alismataceae	11	Cosmopolitan	2	—	*Trop* and *Temp*
Butomaceae	4	Tropics and Temperate	1	—	N. and NE. Qld.
Hydrocharitaceae	13	Tropical and temperate waters	9	1	Tropical coasts, E. Australia and Tas.
Triuridaceae	2	Tropics	1	—	NE. Qld.
Gramineae	556	Cosmopolitan	135	32	General
Cyperaceae	85	Cosmopolitan	41	12	General
Palmae	200	Tropics and Subtropics	20	3	*Trop* and E. Coast
Araceae	107	Tropics and Temperate	9	1	*Trop*
Lemnaceae	4	Cosmopolitan	2	—	
Flagellariaceae	3	Old World Tropics	2	—	*Trop*
Restionaceae	29	S. Africa–Australia	17	12	*Temp* but endemics chiefly *SWP*
Centrolepidaceae	7	SE. Asia and Southern Hemisphere	7	2	*Trop* and *Temp* (esp. latter)
Xyridaceae	2	Tropics and Subtropics	1	—	*Trop* and *Temp*
Eriocaulaceae	9	Tropics and Subtropics	1	—	Tropical Zone and E. Australia
Commelinaceae	29	Tropics and Subtropics	6	—	Mainly *Trop* and E. Australia, 1 in *SWP*
Cartonemataceae	1	Australia	1	1	*Trop*

* According to different authorities.

TABLE 1 (*Continued*)

Family	Total Genera (approx.)	World Distribution	Australia–Tasmania		Chief Distribution of Family in Australia–Tasmania
			Total Genera	Endemic Genera	
Pontederiaceae	6	Tropics	1	—	*Trop* (N. areas)
Philydraceae	4	Malaysia–Australia	4	2	E. Australia but 1 in *SWP*
Juncaceae	8	Temperate, also mountains in Tropics	2	—	Mainly *Temp*
Stemonaceae	3	SE. Asia–Tropical America	1	—	*Trop*
Liliaceae	250	Cosmopolitan	47	30	*Trop* and *SWP*
Haemodoraceae	10	Australia, S. Africa, Tropical America	1	—	*Trop* and *SWP*
Amaryllidaceae	90	Tropics and Subtropics	14	8	*Temp* and E. Australia but 6 endemic *SWP*
Taccaceae	2	Tropics	1	—	*Trop*
Dioscoreaceae	9	Tropics and Subtropics	1	—	*Trop* and *SWP*
Petermanniaceae	1	Australia	1	1	*MMO*
Iridaceae	57	Tropics and Temperate	4	1	*Temp*
Musaceae	6	Tropics	1	—	NE. Qld.
Zingiberaceae	45	Tropics esp. Malaysia	7	—	N. and NE. Qld.
Burmanniaceae	5	Tropics	2	—	NE. Qld. (1); Vic.–Tas. (1)
Orchidaceae	450	Cosmopolitan	75	17	*Trop* and *Temp*
DICOTYLEDONS					
Casuarinaceae	1	Madagascar to SW. Pacific	1	—	General but few spp. in *Er*
Piperaceae	7	Tropics	2	—	NE. Qld. to *MMO*
Balanopsidaceae	1 or 2*	New Caledonia	1	—	NE. Qld.
Fagaceae	5	Three centres of development, one being Australia–N. Zealand–S. America	1	—	SE. Qld. to Tas.
Ulmaceae	13	Tropics and Temperate	2	—	*Trop* to *MMO*
Moraceae	55	Tropics and Subtropics	6	—	*Trop* to *MMO*
Urticaceae	41	Tropics and Temperate	11	—	Mainly NE. *Trop* and E. Australia
Proteaceae	50	Esp. Australia but also Asia and S. Hemisphere	37	28	NE. Qld. (9), Tas. (3), *SWP* (5 endemic)

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* According to different authorities.

TABLE 1 (*Continued*)

Family	Total Genera (approx.)	World Distribution	Australia–Tasmania		Chief Distribution of Family in Australia–Tasmania
			Total Genera	Endemic Genera	
Santalaceae	26	Tropics and Temperate	9	5	*Temp* and *Er*
Opiliaceae	9	Mainly Old World Tropics	2	—	*Trop* and NE. Qld.
Olacaceae	25	Tropics	2	—	N. *Trop* and NE. Qld.
Loranthaceae	36	Tropics and Temperate	12	3	General
Balanophoraceae	15	Indo-Malaysia	1	—	NE. Qld.
Aristolochiaceae	5	Tropics and warm Temperate	1	—	*Trop* and *MMO*
Rafflesiaceae	7	Tropics	1	—	*SWP*
Polygonaceae	40	Chiefly N. Temperate	2	—	*Er* and E. Australia
Chenopodiaceae	75 or 102*	Cosmopolitan	30	19	*Temp* and *Er*, but few *Trop*
Amaranthaceae	90	Tropics and Subtropics	9	2	General
Nyctaginaceae	20	Tropics, esp. America	4	—	*Trop* and *Er*
Gyrostemonaceae	4	Australia	4	4	*Er* and *Temp*
Phytolaccaceae	1	Australia	1	1	*MMO*
Aizoaceae	30–110*	Mainly S. Africa but also Australia, Asia, and America	12	4	All zones
Portulacaceae	17	Cosmopolitan, esp. America	6	—	*Temp* and *Er*, also NE. Qld.
Dysphaniaceae	1	Australia	1	1	*Er*
Caryophyllaceae	80	Cosmopolitan	7	—	*Temp* and dry *Trop*
Nymphaeaceae	8	Tropics and warm Temperate	3	—	*Trop* to E. Australia
Ceratophyllaceae	1	Cosmopolitan	1	—	NE. Qld.
Ranunculaceae	40	Chiefly N. Temperate	5	—	*Temp* and E. Australia
Menispermaceae	65	Tropics and Subtropics	13	5	*Trop* to *MMO* but chiefly NE. Qld. and *MMO*
Winteraceae	5	SE. Asia to S. America	2	—	NE. Qld., E. Australia–Tas.
Austrobaileyaceae	1	NE. Qld.	1	1	NE. Qld.
Calycanthaceae	1	N. America, Asia, Australia	1	—	NE. Qld.
Annonaceae	80	Tropics, esp. in Old World	12	3	Mainly NE. *Trop* to *MMO*
Himantandraceae	1	Indonesia to Australia	1	—	NE. Qld.
Eupomatiaceae	1	NE. Australia–New Guinea	1	—	E. Australia

* According to different authorities.

TABLE 1 (*Continued*)

Family	Total Genera (approx.)	World Distribution	Australia–Tasmania		Chief Distribution of Family in Australia–Tasmania
			Total Genera	Endemic Genera	
Myristicaceae	18	Tropics, esp. Asia	2	—	*Trop*
Monimiaceae	30	S. Tropics, esp. Madagascar, Australia, Polynesia	11	6	NE. Qld. to SE. Australia
Lauraceae	40	Tropics and Subtropics	7	—	Mainly NE. Qld. to *MMO*, also coastal
Hernandiaceae	4	Tropics	3	1	*Trop*
Capparidaceae	40	Tropics and warm Temperate	6	3	General but mainly *Er*
Cruciferae	220–350*	Cosmopolitan	24	15	*Temp* and *Er*
Nepenthaceae	1	Old World Tropics	1	—	NE. Qld.
Byblidaceae	2	S. Africa and Australia	1	—	*SWP* to N. *Trop*
Droseraceae	5	One cosmopolitan, rest local	2	—	Mainly *Temp* but also *Trop*
Podostemonaceae	22	Tropics	1	—	NE. Qld.
Crassulaceae	25	Cosmopolitan	1	—	*Temp* and *Er*
Cephalotaceae	1	*SWP*	1	1	*SWP*
Saxifragaceae	90	Cosmopolitan but chiefly Temperate	9	6	*Temp*
Pittosporaceae	9	Chiefly Australia	9	6	*Trop* and *Temp*
Cunoniaceae	26	S. Tropics and Temperate	13	5	NE. Qld. to Tas.
Davidsoniaceae	1	Australia–Fiji	1	—	NE. Qld. to NE. N.S.W.
Hamamelidaceae	18	Subtropics but discontinuous	2	2	NE. Qld.
Rosaceae	100	Cosmopolitan	7	1	Mainly *Temp* but also *Trop*
Connaraceae	16	Tropics	2	—	NE. Qld.
Leguminosae	600	Cosmopolitan	109	37	General
Geraniaceae	11	Cosmopolitan	3	—	*Temp* to S. *Er*
Oxalidaceae	7	Tropics and Subtropics	1	—	*Temp*
Linaceae	9	Cosmopolitan	2	—	*Temp* to NE. Qld.
Erythroxylaceae	2	Tropics, esp. America	1	—	*Trop*
Zygophyllaceae	22	Tropics and Subtropics	4	—	*Er* and dry *Temp*
Rutaceae	100	Tropics and Temperate, esp. S. Africa and Australia	35	20	*Temp* and *Trop*, but esp. *SWP*
Simaroubaceae	28	Tropics and Subtropics	8	3	NE. Qld. to *MMO*

* According to different authorities.

TABLE 1 (*Continued*)

Family	Total Genera (approx.)	World Distribution	Australia–Tasmania		Chief Distribution of Family in Australia–Tasmania
			Total Genera	Endemic Genera	
Burseraceae	13	Tropics	2	—	NE. *Trop*
Meliaceae	40	Tropics and Subtropics	14	3	*Trop* including drier areas
Malpighiaceae	55	Tropics, esp. S. America	2	—	NE. Qld.
Tremandraceae	3	Australia	3	3	*Temp*, mainly *SWP*
Polygalaceae	10	Cosmopolitan except New Zealand, and Polynesia, and Arctic	4	1	*Trop* and *Temp*
Dichapetalaceae	3	Tropics	1	—	NE. Qld.
Euphorbiaceae	220	Cosmopolitan	47	15	General
Callitrichaceae	1	Cosmopolitan	1	—	*Temp*
Anacardiaceae	60	Mainly Tropics	7	2	N. and E. *Trop*
Corynocarpaceae	1	Australia–New Caledonia, New Zealand	1	—	NE. Qld.
Aquifoliaceae	5	Tropics and Temperate	2	—	NE. and E. Qld.
Celastraceae	38	Tropics and Temperate	12	5	*Trop*, mainly NE. Qld. but 1 *SWP*
Hippocrateaceae	3	Tropics and Subtropics	3	—	E. *Trop*
Stackhousiaceae	2	Malaysia–New Zealand	2	1	Widespread but only the endemic in *Er*
Icacinaceae	38	Tropics	4	1	NE. Qld. to *MMO*
Akaniaceae	1	E. Australia	1	1	*MMO*
Irvingbaileyaceae	1	NE. Queensland	1	1	NE. Qld.
Sapindaceae	120	Tropics and Subtropics	25	7	General but mainly *Trop* in NE. and E. Qld.
Cardipteridaceae	1	Asia–Australia	1	—	NE. Qld.
Rhamnaceae	40	Cosmopolitan	16	7	General but mainly *Trop* and *Temp*
Vitaceae	10	Tropics and warm Temperate	6	1	Mainly *Trop* but 1 *SWP*
Elaeocarpaceae	7	Tropics and Subtropics	5	1	Mainly N. and E. *Trop* but esp. NE. Qld.
Tiliaceae	35	Tropics and Temperate	6	—	*Trop* and N. *Er*
Malvaceae	35	Tropics and Temperate	15	4	General, but esp. *Trop* and *Er*
Bombaceae	20	Tropics, esp. America	3	—	*Trop*

TABLE 1 (*Continued*)

Family	Total Genera (approx.)	World Distribution	Australia–Tasmania		Chief Distribution of Family in Australia–Tasmania
			Total Genera	Endemic Genera	
Sterculiaceae	48	Chiefly Tropics	21	10	General but less frequent in *Er*
Dilleniaceae	12	Tropics and Subtropics	4	1	Chiefly *Temp* but also NE. *Trop*
Actinidiaceae	4	E. Asia–Australia	1	—	NE. Qld.
Eucryphiaceae	2	Australia–New Caledonia–S. America	1	—	E. Australia–Tas.
Ochnaceae	20	Tropics	1	—	NE. Qld.
Theaceae	24	Tropics and Subtropics	1	—	NE. Qld.
Guttiferae	42	Chiefly Tropics	5	—	*Temp* and *Trop*
Elatinaceae	2	Tropics and Temperate	2	—	General
Frankeniaceae	4	Tropics and Temperate	1	—	Mainly *Er* and *Temp*
Cochlospermaceae	3	Tropics	1	—	*Trop*
Violaceae	15	Cosmopolitan	5	1	Mainly *Temp* but 1 widespread in *Trop* and *Er*
Flacourtiaceae	15	Tropics and Subtropics	7	2	NE. Qld. to *MMO*
Passifloraceae	12	Tropics and warm Temperate	2	—	*Trop*
Thymelaeaceae	38	Tropics and Subtropics, esp. Africa	6	1	Widespread esp. (1 genus) *Temp*
Elaeagnaceae	3	Mainly N. Hemisphere	1	—	NE. Qld.
Lythraceae	21	Cosmopolitan except cold regions	7	—	Widespread except in *Er*
Sonneratiaceae	3	Tropical Asia, Africa	1	—	*Trop*
Lecythidaceae	18	Tropics	2	—	*Trop*
Rhizophoraceae	12	Esp. Old World Tropics	4	—	*Trop* and warm coasts
Alangiaceae	1	Old World Tropics	1	—	E. *Trop*
Combretaceae	16	Tropics and Subtropics	3	—	*Trop*
Myrtaceae	90	Chief centres America and Australia	47	33	General but fewer in *Er*, 15 endemic *SWP*
Melastomaceae	200	Tropics and Subtropics	5	—	*Trop*, esp. N. and E.
Onagraceae	40	Tropics and Temperate	4	—	*Trop* and *Temp*

TABLE 1 (*Continued*)

Family	Total Genera (approx.)	World Distribution	Australia–Tasmania		Chief Distribution of Family in Australia–Tasmania
			Total Genera	Endemic Genera	
Haloragaceae	7	Cosmopolitan	5	2	General but mainly *Temp*
Araliaceae	55	Tropics esp. Indo-Malaysia	12	3	Mainly *Trop* but 1 Hamersley Range, W.A., and 2 to SE. Australia
Umbelliferae	200	Cosmopolitan	23	9	Mainly *Temp* and *Er*
Ericaceae	50	Cosmopolitan	5	1	NE. Qld. to Tas.
Epacridaceae	30	Mainly Australia but also Malaysia to S. America	28	21	*Temp* and E. Australia but 7 endemic *SWP*
Myrsinaceae	35	Tropics and Subtropics	6	—	NE. *Trop* to Vic.
Primulaceae	25	Cosmopolitan but esp. N. Temperate	2	—	*Temp*, esp. SE. Australia
Plumbaginaceae	10	Cosmopolitan esp. salt areas and coastal	3	—	*Trop* (mainly)
Sapotaceae	35	Tropics	9	2	*Trop* and *MMO*
Ebenaceae	7	Tropics esp. Indo-Malaysia	1	—	NE. *Trop*
Symplocaceae	1	Tropics and Subtropics	1	—	NE. Qld. to E. N.S.W.
Oleaceae	21	Tropics and warm Temperate	6	—	*Trop* to SE. Australia
Loganiaceae	35	Tropics and warm Temperate	7	1	Mainly *Trop* but also *Temp*
Gentianaceae	80	Cosmopolitan	7	—	Mainly *Temp*, esp. SE. Australia but also *SWP*, Tas., and *Trop*
Apocynaceae	180	Mainly Tropics	11	1	*Trop*, N. *Er*, E. Australia, and S. coast
Asclepiadaceae	320	Mainly Tropics	14	2	*Trop* and *Er*
Convolvulaceae	50	Tropics and Temperate	19	2	Mainly *Trop* but in all Zones
Hydrophyllaceae	18	Cosmopolitan	1	—	*Trop*
Boraginaceae	100	Tropics and Temperate	13	3	All Zones
Verbenaceae	70	Tropics and Temperate	24	13	*Trop*, *Er*, and *SWP*
Labiatae	200	Cosmopolitan	21	6	All Zones but mainly *Trop*
Solanaceae	85	Tropics and Temperate, esp. Central and S. America	8	3	All Zones but mainly *Trop* and *Er*

TABLE 1 (*Continued*)

Family	Total Genera (approx.)	World Distribution	Australia–Tasmania		Chief Distribution of Family in Australia–Tasmania
			Total Genera	Endemic Genera	
Scrophulariaceae	200	Cosmopolitan	28	2	Mainly *Trop* and E. Australia
Bignoniaceae	100	Tropics	6	1	*Trop* and *Er* Zones to E. Australia
Pedaliaceae	14	Tropics, S. Africa, Madagascar–Malaysia	2	1	Arid parts of *Trop* and *Er*
Orobanchaceae	12	Chiefly N.–Temperate Old World	1	—	*Temp* (possibly not native)
Gesneriaceae	85	Tropics and Subtropics	5	1	NE. Qld. and E. Australia
Lentibulariaceae	10	Cosmopolitan	2	—	*Trop* and *Temp* Zones
Acanthaceae	240	Mainly Tropics	15	2	N. and E. *Trop* but reaching *Er*
Myporaceae	5	Chiefly Australia but also Asia, Africa, and Pacific	2	1	Widespread especially in *Er*
Plantaginaceae	3	Cosmopolitan	1	—	General
Rubiaceae	450	Tropics and Temperate	36	5	Mainly *Trop* but also *Temp* and *Er*
Caprifoliaceae	18	Temperate	1	—	*Temp*
Cucurbitaceae	90	Tropics and Subtropics	11	—	*Trop* and *Er*
Campanulaceae	60	Tropics and Temperate	7	—	E. Australia and *Temp*, few *Trop*
Sphenocleaceae	1	Tropics	1	—	N. *Trop*
Goodeniaceae	13	Chiefly Australia but also Asia–New Zealand	13	10	General but 5 endemic *SWP*
Brunoniaceae	1	Australia	1	1	*Er* and dry *Temp*
Stylidiaceae	6	Tropical Asia to S. America	4	1	*Trop* and *Temp*
Compositae	900	Cosmopolitan	104	55	General
Total	9800 (approx.)		1700	566	

Of the families listed the following are restricted to the Australian Region:

- Cartonemataceae
- Petermanniaceae
- Dysphaniaceae: monogeneric, usually placed under Chenopodiaceae by Australian authors
- Gyrostemonaceae: genera formerly under Phytolaccaceae
- Austrobaileyaceae: monotypic
- Cephalotaceae: monotypic
- Tremandraceae
- Akaniaceae: monotypic
- Irvingbaileyaceae: monotypic
- Brunoniaceae: monotypic

The following families have their major centres of development within the Australian Region though they are not wholly restricted to it:

- Eupomatiaceae
- Pittosporaceae
- Stackhousiaceae
- Epacridaceae
- Myoporaceae
- Goodeniaceae

In a number of families the relative number of endemic genera indicates that they have been in the Region for a long period of time. As will be seen from Table 2 all these families are widespread within the Region. In some cases the local divergence has led to the recognition of distinct families by some authors.

- Gramineae
- Cyperaceae
- Liliaceae: Xanthorrhoeaceae, of eight genera one of which is also in New Caledonia, is recognized by Hutchinson who also transfers two genera to the Philesiaceae
- Amaryllidaceae: The tribe Conostyleae is placed in Haemodoraceae by Hutchinson
- Proteaceae: both the subfamilies Persoonoideae and Grevilleoideae are well represented
- Santalaceae
- Saxifragaceae
- Cunoniaceae
- Leguminosae: especially the tribe Podalyrieae
- Rutaceae
- Myrtaceae: especially the Leptospermoideae and Chamelaucoideae, the latter being restricted to the Region
- Verbenaceae: the tribe Chloantheae is endemic and restricted
- Compositae: especially genera in the Inuleae

It might perhaps have been advisable to include with the above the Loranthaceae, Chenopodiaceae, and Cruciferae but as the number of generic units is dependent on the acceptance of recent treatments with which not all may agree such a placing must be provisional.

It should also be noted that no less than 20 families are limited in their representation to the North-East Queensland area, i.e. to the eastern parts of the Cape York Peninsula. Apart from two endemic families, these are all well represented in the Malaysian Region and they serve to illustrate the importance of this area as a portal through which migration, both in and out of the Australian Region, has undoubtedly occurred. The intermingling of Malaysian and Australian elements in the Tropical Zone is evidence in favour of the first and the occurrence of Australian genera such as *Callitris*, *Banksia*, and *Eucalyptus* in New Guinea, and of *Eucalyptus*, *Stackhousia*, *Stylidium*, and *Styphelia* in other parts of the Malaysian Region, indicates the latter.

In contrast to the relative importance of these tropical families the low number of families which are wholly temperate in their occurrence and which are represented only in the Temperate Zone is a peculiar feature. Those families which are well represented in the Temperate Zone are either widespread throughout the world or are also found in the tropics and subtropics.

It is customary to regard the Australian flora as consisting of three main elements: The Australian or Autochthonian, the Antarctic, and the Malaysian (sometimes called the Indo-Malayan or even the Indo-Melanesian). The influence of Malaysian elements is obvious from the above and speculation concerning the Antarctic elements can be mainly left until the final part of this study. Such speculations are largely based on affinities with the floras of New Zealand, South America, and, to a lesser degree, South Africa. There remain a number of genera which are temperate in their requirements and which, judging by their world distribution and their occurrence in Australia, are as likely to have reached Australia from a northern source as from a southern or antarctic one. Just how such a migration, as this would involve, could have taken place remains a mystery but an interesting account of the problems involved is given by van Steenis's study of the temperate flora of the mountain areas in Malaysia (1934*a*, 1934*b*, 1936).

In Table 2 the genera are presented under their families according to the occurrence within particular zones. As was to be expected the distribution shows that some are found in particular areas of a single zone, some occur throughout a zone and others may be found in more than one zone. Consequently in analysing the distribution patterns it is necessary to allow for these variations. The genera present in the Interzones have not been specially analysed but Interzone 1 will be discussed in a later portion dealing with the South-West Province of Western Australia. The data concerning Interzones 2 and 3 are not adequate for a comparable treatment and as they are not true floristic units an analysis could give a misleading picture of the representation and of the mosaic character of the distribution. In the Table the vertical columns, numbered from (1) to (18), represent the different subdivisions as follows:

(1) Temperate Zone—total (sum of columns 2–8)
(2) Temperate Zone—residue after exclusion of genera in columns 3–8
(3) South-West Province of Western Australia only
(4) Tasmania only
(5) Temperate and Tropical Zones (i.e. genera occurring in both)
(6) Temperate and Eremaean Zones
(7) Temperate Zone and MacPherson–Macleay Overlap
(8) All Zones—i.e. occurring throughout the Region
(9) Tropical Zone—total (sum of columns 5, 8, 10–13)
(10) Tropical Zone—residue after exclusion of genera in columns 5, 8, 11–13
(11) North-East Queensland only
(12) Tropical Zone and MacPherson–Macleay Overlap
(13) Tropical and Eremaean Zones
(14) Eremaean Zone—total (sum of columns 6, 8, 13, 15, 16)
(15) Eremaean Zone only
(16) Eremaean Zone and MacPherson–Macleay Overlap
(17) MacPherson–Macleay Overlap—total. This includes only some of the genera in columns 5 and 8. A fuller analysis will be given later
(18) MacPherson–Macleay Overlap only

The data in Table 2 show the importance of the South-West Province of Western Australia and the part played by genera which occur in both the Tropical and Temperate Zones in the total for the Temperate Zone. Under the Tropical Zone it is clear that the flora of North-East Queensland is as rich in genera as it is in families.

In Table 3 the data from Table 2 are analysed under endemic and non-endemic and according to the number of species per genus. Throughout this paper the term "endemic" indicates genera or species which are restricted to the Australian Region. Where the genus is itself restricted to a particular area within the Region it naturally follows that the species in it are also so limited. "Non-endemic" is used here to refer to genera or species which occur both within the Australian Region and in other lands. Since naturalized plants have been excluded from this analysis the term "non-endemic" does not cover species which have been introduced by man and which have not become fully established in wholly native communities. Doubtless man has long been an influence in the introduction of plants on the north coast but it would be difficult to distinguish those resulting from early visitations as they have been fully absorbed.

It will be noted in Table 3 that the smaller genera are in the majority, in accordance with the remarks of Good (1953, p.79) concerning relative numbers of species and sizes of genera. In the total flora for each area there is a spread over the size groups, the larger being fewer than the smaller and the series forming the hollow curve discussed by Willis (1949).

TABLE 2

OCCURRENCE IN AREAS OF THE AUSTRALIAN REGION. NUMBERS OF GENERA ARRANGED UNDER FAMILIES

Temp, Temperate Zone; *Trop*, Tropical Zone; *Er*, Eremaean Zone; *MMO*, MacPherson–Macleay Overlap; *SWP*, South-West Province of Western Australia

Family	(1) *Temp* Total	(2) *Temp* Residue	(3) *SWP*	(4) Tas. Only	(5) *Temp* + *Trop*	(6) *Temp* + *Er*	(7) *Temp* + *MMO*	(8) All Zones	(9) *Trop* Total	(10) *Trop* Residue	(11) NE. Qld. Only	(12) *Trop* + *MMO*	(13) *Trop* + *Er*	(14) *Er* Total	(15) *Er* Only	(16) *Er* + *MMO*	(17) *MMO* Total	(18) *MMO* Only
GYMNOSPERMS	10	1	1	5	2			1	7	3		1		1			4	
MONOCOTYLEDONS																		
Typhaceae	1				1				1								1	
Pandanaceae									2	1		1					1	
Sparganiaceae	1						1										1	
Potamogetonaceae	6	3			1		1	1	3	1				1			2	
Najadaceae									1			1					1	
Aponogetonaceae									1			1					1	
Scheuchzeriaceae	1							1	1					1			2	1
Alismataceae	2				1			1	2					1			2	
Butomaceae									1	1								
Hydrocharitaceae	4				4				8	3	1						5	1
Triuridaceae									1		1							
Gramineae	49	8	2		9	5	12	13	94	28	12	16	17	43	8	1	69	4
Cyperaceae	24	3	3		8		6	4	27	4	5	5	1	6	1		24	1
Palmae									21	7	9	3	1	1			4	
Araceae	1						1		8	5	1	2					3	
Lemnaceae	2	1					1										1	
Flagellariaceae									2	1		1					1	
Restionaceae	16	2	10		2		2		2								5	1
Centrolepidaceae	7	3	1	1	1	1			1					1			1	
Xyridaceae	1				1				1								1	
Eriocaulaceae	1							1	1					1			1	

TABLE 2 (*Continued*)

Family	(1) *Temp* Total	(2) *Temp* Residue	(3) *SWP*	(4) Tas. Only	(5) *Temp* + *Trop*	(6) *Temp* + *Er*	(7) *Temp* + *MMO*	(8) All Zones	(9) *Trop* Total	(10) *Trop* Residue	(11) NE. Qld. Only	(12) *Trop* + *MMO*	(13) *Trop* + *Er*	(14) *Er* Total	(15) *Er* Only	(16) *Er* + *MMO*	(17) *MMO* Total	(18) *MMO* Only
Commelinaceae	1				1				6	1	1	2	1	1			4	
Cartonemataceae	1				1				1									
Pontederiaceae									1	1								
Philydraceae	2		1		1				2			1					3	1
Juncaceae	2						2										2	
Stemonaceae									1	1								
Liliaceae	43	6	12	1	11	2	9	2	16	2		1		5			23	1
Haemodoraceae	1				1				1								1	
Amaryllidaceae	10	1	6	1	1	1			4			2	1	1			5	1
Taccaceae									1	1								
Dioscoreaceae	1				1				1								1	
Iridaceae	4	1	1				2										2	
Petermanniaceae																	1	1
Musaceae									1		1							
Zingiberaceae									7	1	5	1					1	
Burmanniaceae	1	1							1	1								
Orchidaceae	32	4	4		8		16		47	7	22	10					38	4
DICOTYLEDONS																		
Casuarinaceae	1							1	1					1			1	
Piperaceae									2			2					2	
Balanopsidaceae									1		1							
Fagaceae	1						1										1	
Ulmaceae	1				1				2			1					1	
Moraceae	1				1				6	1	1	2	1	1			4	
Urticaceae	3						2	1	8	3	1	3		1			7	1

TABLE 2 (*Continued*)

Family	(1) *Temp* Total	(2) *Temp* Residue	(3) *SWP*	(4) Tas. Only	(5) *Temp* + *Trop*	(6) *Temp* + *Er*	(7) *Temp* + *MMO*	(8) All Zones	(9) *Trop* Total	(10) *Trop* Residue	(11) NE. Qld. Only	(12) *Trop* + *MMO*	(13) *Trop* + *Er*	(14) *Er* Total	(15) *Er* Only	(16) *Er* + *MMO*	(17) *MMO* Total	(18) *MMO* Only
Proteaceae	22	3	4	3	5		5	2	22		10	5		2			17	
Santalaceae	7					3	3	1	2		1			5	1		6	
Opiliaceae									2	1	1							
Olacaceae	1				1				2	1							1	
Loranthaceae	6	1	1				1	3	7			3	1	5	1	1	8	
Balanophoraceae									1		1							
Aristolochiaceae									1			1					1	
Rafflesiaceae	1		1															
Polygonaceae	2							2	2					2			2	
Chenopodiaceae	13	2	3		1	5	1	1	3	1				22	16		6	
Amaranthaceae	2							2	7	2	1	1	1	4	1		5	1
Nyctaginaceae	1				1				4	1		1	1	1			3	
Phytolaccaceae									1			1					1	
Gyrostemonaceae	4		1			3								3			1	
Aizoaceae	5	2				1	2		3			1	2	7	4		5	
Portulacaceae	5	3				2			1		1			2			1	
Dysphaniaceae														1	1			
Caryophyllaceae	6	2				1	3		1				1	2			3	
Nymphaeaceae									3	1		2					2	
Ceratophyllaceae									1			1					1	
Ranunculaceae	5	1		1		1	2							1			2	
Menispermaceae	1				1				9	3	4	1					6	4
Winteraceae	1				1				2		1						1	
Austrobaileyaceae									1		1							
Calycanthaceae									1		1							
Annonaceae									11	3	4	4					5	1

TABLE 2 (*Continued*)

Family	(1) *Temp* Total	(2) *Temp* Residue	(3) *SWP*	(4) Tas. Only	(5) *Temp* + *Trop*	(6) *Temp* + *Er*	(7) *Temp* + *MMO*	(8) All Zones	(9) *Trop* Total	(10) *Trop* Residue	(11) NE. Qld. Only	(12) *Trop* + *MMO*	(13) *Trop* + *Er*	(14) *Er* Total	(15) *Er* Only	(16) *Er* + *MMO*	(17) *MMO* Total	(18) *MMO* Only
Himantandraceae									1		1							
Eupomatiaceae	1				1				1								1	
Myristacaceae									2	2								
Monimiaceae	3				2		1		8		4	2					7	2
Lauraceae	1				1				7			6					7	
Hernandiaceae									3	2	1							
Capparidaceae	1		1						4	1	1		2	3	1		2	
Cruciferae	12	3		1		4	4							16	12		5	
Nepenthaceae									1		1							
Byblidaceae	1				1				1									
Droseraceae	1				1				2	1							1	
Podostemonaceae									1		1							
Crassulaceae	1					1								1			1	
Cephalotaceae	1		1															
Saxifragaceae	5		1	1	1		2		4			3					7	1
Pittosporaceae	7		2			1	3	1	3			2		2			7	
Cunoniaceae	4	1		1			2		8		3	5					8	1
Davidsoniaceae									1			1					1	
Hamamelidaceae									2		2							
Rosaceae	5	1	1		1		2		3	1	1						3	
Connaraceae									2		2							
Leguminosae	42	2	4		7	5	12	12	82	27	15	14	7	28	4		48	
Geraniaceae	3					1	2							1			3	
Oxalidaceae	1	1																
Linaceae	1						1		1		1						1	
Erythroxylaceae									1	1								

TABLE 2 (*Continued*)

Family	(1) *Temp* Total	(2) *Temp* Residue	(3) *SWP*	(4) Tas. Only	(5) *Temp* + *Trop*	(6) *Temp* + *Er*	(7) *Temp* + *MMO*	(8) All Zones	(9) *Trop* Total	(10) *Trop* Residue	(11) NE. Qld. Only	(12) *Trop* + *MMO*	(13) *Trop* + *Er*	(14) *Er* Total	(15) *Er* Only	(16) *Er* + *MMO*	(17) *MMO* Total	(18) *MMO* Only
Zygophyllaceae	3					2		1	2				1	5			1	
Rutaceae	16	2	5	1	3		5		18	3	1	8	3	2			22	4
Simaroubaceae									7	4	1	2					3	1
Burseraceae									2	2								
Meliaceae	2				2				14	4	3	4	1	1			7	
Malpighiaceae									2		2							
Tremandraceae	3		2				1										1	
Polygalaceae	2				1	1			3		1	1		1			3	
Dichapetalaceae									1		1							
Euphorbiaceae	14		2		3	1	5	3	38	8	8	16		4			29	1
Callitrichaceae	1						1										1	
Anacardiaceae									6	4	1	1					2	1
Corynocarpaceae									1		1							
Aquifoliaceae									2	2								
Celastraceae	1		1						11		6	5					5	
Hippocrateaceae									3	1	2							
Stackhousiaceae	1				1				1					1	1		1	
Icacinaceae									4		3	1					1	
Akaniaceae																	1	1
Irvingbaileyaceae									1		1							
Sapindaceae	2					1		1	21	4	4	11	1	4	1		14	2
Cardiopteridaceae									1		1							
Rhamnaceae	8	2	1		1		4		8	3	2	1	1	2	1		6	
Vitaceae	2		1		1				4	2		1					3	1
Elaeocarpaceae	2				2				5		2	1					3	
Tiliaceae									5	1	1	1	2	2			3	1

TABLE 2 (*Continued*)

Family	(1) *Temp* Total	(2) *Temp* Residue	(3) *SWP*	(4) Tas. Only	(5) *Temp* + *Trop*	(6) *Temp* + *Er*	(7) *Temp* + *MMO*	(8) All Zones	(9) *Trop* Total	(10) *Trop* Residue	(11) NE. Qld. Only	(12) *Trop* + *MMO*	(13) *Trop* + *Er*	(14) *Er* Total	(15) *Er* Only	(16) *Er* + *MMO*	(17) *MMO* Total	(18) *MMO* Only
Malvaceae	5	1				3	1		9	4			5	9	1		6	
Bombacaceae									3	3				1				
Sterculiaceae	7	2	2			1		2	13	5	1	2	3	7	2		8	1
Dilleniaceae	1						1		3	2	1						1	
Actinidiaceae									1		1							
Eucryphiaceae	1	1																
Ochnaceae									1		1							
Theaceae									1		1							
Guttiferae	1				1				5	1	3						1	
Elatinaceae	1				1				2				1	1			2	
Frankeniaceae	1					1								1				
Cochlospermaceae									1	1								
Violaceae	3	1					1	1	2		1			2	1		2	
Flacourtiaceae									6	2	3	1					2	1
Passifloraceae									2	1		1					1	
Thymelaeaceae	2			1				1	4		1	2		1			4	1
Elaeagnaceae									1		1							
Lythraceae	1						1		6	4	1		1	1			2	
Sonneratiaceae									1	1								
Lecythidaceae									2	2								
Rhizophoraceae									4	2		2					2	
Alangiaceae									1			1					1	
Combretaceae									3	3								
Myrtaceae	32	1	13		4	4	7	3	18	7		4		9	2		20	2
Melastomaceae									5	2	2	1					1	
Onagraceae	3			1	1		1		2	1							2	

TABLE 2 (*Continued*)

Family	(1) *Temp* Total	(2) *Temp* Residue	(3) *SWP*	(4) Tas. Only	(5) *Temp* + *Trop*	(6) *Temp* + *Er*	(7) *Temp* + *MMO*	(8) All Zones	(9) *Trop* Total	(10) *Trop* Residue	(11) NE. Qld. Only	(12) *Trop* + *MMO*	(13) *Trop* + *Er*	(14) *Er* Total	(15) *Er* Only	(16) *Er* + *MMO*	(17) *MMO* Total	(18) *MMO* Only
Haloragaceae	5		1	1	1	1		1	2					2			2	
Araliaceae	2				2				11	4	4	1					4	1
Umbelliferae	20	7	2		2	3	5	1	4		1			6	2		11	
Ericaceae	3	1		1			1		2		2						1	
Epacridaceae	28	6	7	2	4		9		4								12	
Myrsinaceae	1				1				6		2	3					4	
Primulaceae	2					1	1							1			2	
Plumbaginaceae	1				1				3	1		1					2	
Sapotaceae									8	2	4	2					3	1
Ebenaceae									1			1					1	
Symplocaceae									1			1					1	
Oleaceae	3	1			1			1	5	1	1	1		1			3	
Loganiaceae	2				1		1		6	3	2						2	
Gentianaceae	6	1		1	1		2	1	3	1				1			4	
Apocynaceae	2				2				10	1	2	4	1	2	1		7	
Asclepiadaceae	2				1			1	12	4	2	2	2	5	2		6	
Convolvulaceae	8		1		1	1	1	4	16	4	4		3	8			8	
Hydrophyllaceae									1	1								
Boraginaceae	2						1	1	8	4		1	2	7	4		4	
Verbenaceae	5		3		1	1			15	4	2	6	2	7	4		10	1
Labiatae	11	1	1		2	3	4		11	5	3	1		4	1		8	
Solanaceae	4					2		2	3	1				7	3		4	
Scrophulariaceae	9			1		1	7		19	9	1	6	3	4			16	
Bignoniaceae	1							1	6	2	3			1			1	
Pedaliaceae									1				1	2	1			
Orobanchaceae	1	1																

TABLE 2 (*Continued*)

Family	(1) *Temp* Total	(2) *Temp* Resi-due	(3) *SWP*	(4) Tas. Only	(5) *Temp* + *Trop*	(6) *Temp* + *Er*	(7) *Temp* + *MMO*	(8) All Zones	(9) *Trop* Total	(10) *Trop* Resi-due	(11) NE. Qld. Only	(12) *Trop* + *MMO*	(13) *Trop* + *Er*	(14) *Er* Total	(15) *Er* Only	(16) *Er* + *MMO*	(17) *MMO* Total	(18) *MMO* Only
Gesneriaceae	1						1		4		4						1	
Lentibulariaceae	2	1			1				1								1	
Acanthaceae	1				1				13	9	1	1	1	3	2		3	
Myoporaceae	2					1		1	1					[illegible]			1	
Plantaginaceae	1					1								1			1	
Rubiaceae	7	2			1	1	3		30	11	9	6	3	4			13	
Caprifoliaceae	1						1										1	
Cucurbitaceae	1				1				10	5		1	3	4	1		4	
Campanulaceae	7	2	1		1		1	2	3					2			4	
Sphenocleaceae									1	1								
Goodeniaceae	10	1	4		1	1		3	6	1			1	6	1		4	
Brunoniaceae	1					1								1			1	
Stylidiaceae	4			2	1		1		1								2	
Compositae	57	12	3	2	3	22	7	8	33	10	2	7	3	54	21		42	4
Total	731	102	111	28	134	91	176	89	1037	284	227	222	81	363	102	2	761	51

TABLE 3

OCCURRENCE IN AREAS OF THE AUSTRALIAN REGION. GENERA ARRANGED ACCORDING TO ENDEMISM AND SIZE

Temp, Temperate Zone; *Trop*, Tropical Zone; *Er*, Eremaean Zone; *MMO*, MacPherson–Macleay Overlap; *SWP*, South-West Province of Western Australia; Σ, Regional total

Numerals in parentheses in the second part of this Table represent the number of genera with endemic species only

	Temp Total	*Temp* Residue	*SWP*	Tas. Only	*Temp* + *Trop*	*Temp* + *Er*	*Temp* + *MMO*	All Zones	*Trop* Total	*Trop* Residue	NE. Qld. Only	*Trop* + *MMO*	*Trop* + *Er*	*Er* Total	*Er* Only	*Er* + *MMO*	*MMO* Total	*MMO* Only	Σ
ENDEMIC GENERA																			
(Total)	341	52	105	14	26	53	76	15	146	39	36	23	7	161	86	—	191	34	566
Monotypic	97	19	48	13	1	5	11	—	67	28	30	7	1	53	47	—	50	28	238
2–5 spp.	118	21	39	1	10	18	27	3	49	11	6	15	4	52	27	—	64	6	188
6–10 spp.	46	4	11	—	6	12	10	3	12	—	—	1	2	23	6	—	25	—	55
11–20 spp.	38	4	4	—	6	7	14	3	9	—	—	—	—	15	5	—	25	—	43
21–30 spp.	16	2	1	—	2	4	6	1	3	—	—	—	—	6	1	—	11	—	17
31–40 spp.	9	2	1	—	—	2	4	—	—	—	—	—	—	2	—	—	4	—	9
41–50 spp.	7	—	—	—	1	1	2	3	4	—	—	—	—	4	—	—	5	—	7
51–60 spp.	2	—	1	—	—	1	—	—	—	—	—	—	—	1	—	—	1	—	2
61–70 spp.	3	—	—	—	—	2	1	—	—	—	—	—	—	2	—	—	3	—	3
71–80 spp.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
81–90 spp.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
91–100 spp.	2	—	—	—	—	1	1	—	—	—	—	—	—	1	—	—	1	—	2
Over 100 spp.	2	—	—	—	—	—	—	2	2	—	—	—	—	2	—	—	2	—	2
NON-ENDEMIC GENERA (Total)	390	50	6	14	108	38	100	74	891	245	191	199	74	202	16	2	570	17	1134
Monotypic	11	2	1	1	5	—	2	—	44	24	10	4	1	1	—	—	12	1	51
Restricted to 1 endemic sp.	36	12	3	9	2	2	5	3	121	29	74	10	3	12	4	—	27	9	165

TABLE 3 (*Continued*)

	Temp Total	*Temp* Residue	*SWP*	Tas. Only	*Temp* + *Trop*	*Temp* + *Er*	*Temp* + *MMO*	All Zones	*Trop* Total	*Trop* Residue	NE. Qld. Only	*Trop* + *MMO*	*Trop* + *Er*	*Er* Total	*Er* Only	*Er* + *MMO*	*MMO* Total	*MMO* Only	Σ
Restricted to 1 non-endemic sp.	40	8	2	2	11	4	10	3	195	70	76	29	5	14	2	—	61	5	227
2–5 spp.	131	26	—	2	41	9	44	9	320	106	30	106	27	53	8	2	227	2	412
	(43)	(15)	—	(2)	(11)	(1)	(12)	(2)	(116)	(33)	(17)	(41)	(12)	(22)	(7)	(2)	(78)	(2)	
6–10 spp.	57	2	—	—	14	6	16	19	100	13	1	34	18	43	—	—	101	—	123
	(26)	—	—	—	(9)	(3)	(9)	(5)	(38)	(1)	(1)	(16)	(6)	(14)	—	—	(43)	—	
11–20 spp.	45	—	—	—	16	5	10	13	56	2	—	13	12	30	—	—	65	—	71
	(20)	—	—	—	(8)	(1)	(7)	(4)	(19)	—	—	(5)	(2)	(6)	—	—	(30)	—	
21–30 spp.	16	—	—	—	5	4	3	4	17	1	—	3	4	12	—	—	20	—	24
	(6)	—	—	—	(1)	(4)	(1)	—	(3)	—	—	(2)	—	(4)	—	—	(9)	—	
31–40 spp.	17	—	—	—	4	3	4	6	12	—	—	—	2	12	1	—	18	—	20
	(7)	—	—	—	—	(2)	(3)	(2)	(2)	—	—	—	—	(4)	—	—	(6)	—	
41–50 spp.	7	—	—	—	2	1	1	3	7	—	—	—	2	7	1	—	8	—	10
	(1)	—	—	—	—	—	—	(1)	(1)	—	—	—	—	(1)	—	—	(1)	—	
51–60 spp.	7	—	—	—	2	3	—	2	4	—	—	—	—	5	—	—	7	—	7
	(3)	—	—	—	—	(3)	—	—	—	—	—	—	—	(3)	—	—	(3)	—	
61–70 spp.	6	—	—	—	2	—	2	2	4	—	—	—	—	2	—	—	6	—	6
	(3)	—	—	—	(2)	—	(1)	—	(2)	—	—	—	—	—	—	—	(3)	—	
71–80 spp.	6	—	—	—	2	1	—	3	5	—	—	—	—	4	—	—	6	—	6
	(1)	—	—	—	(1)	—	—	—	(1)	—	—	—	—	—	—	—	(2)	—	
81–90 spp.	2	—	—	—	—	—	1	1	1	—	—	—	—	1	—	—	2	—	2
	(1)	—	—	—	—	—	(1)	—	—	—	—	—	—	—	—	—	—	—	
91–100 spp.	3	—	—	—	—	—	2	1	1	—	—	—	—	1	—	—	3	—	3
Over 100 spp.	7	—	—	—	2	—	—	5	7	—	—	—	—	5	—	—	7	—	7
	(3)	—	—	—	(2)	—	—	(1)	(3)	—	—	—	—	(1)	—	—	(3)	—	
Total	731	102	111	28	134	91	176	89	1037	284	227	222	81	363	102	2	761	51	1700

From the first part of the table the proportion of endemic genera when calculated from the total for each Zone is as follows:

Temperate Zone	46·6 per cent.
Tropical Zone	14·0 per cent.
Eremaean Zone	47·1 per cent.

The number of endemic genera in the Temperate Zone is much influenced by those restricted to the South-West Province of Western Australia. These represent 30·8 per cent. of the total endemics of the Zone. On the other hand the figure for the Eremaean Zone is affected by the inclusion of the minor genera recognized in the Chenopodiaceae and the Cruciferae. The number of genera restricted to Tasmania is low but had there been enough data on distribution in Victoria, particularly the more elevated areas of the Australian Alps, it might have been possible to recognize a "Tasmanian Subzone" as a satisfactory phytogeographic unit.

The fact that the endemic genera restricted to the MacPherson–Macleay Overlap amount to 34, or 10·6 per cent. of the Overlap total, is of some interest. It can hardly be doubted that the varying topography and the varying stresses resulting from the coincidence of the two climatic systems have combined to produce conditions as well as a multiplicity of habitats favourable for the survival of newly evolved forms or the persistence of those lost elsewhere under major changes of climate. This area may be regarded as a refugium of a special kind and of particular interest for the phytogeographer.

Turning to the part of Table 3 which deals with non-endemic genera it is obvious that the relative proportions shown amongst endemic genera are reversed and that much the highest number are to be found in the Tropical Zone. Furthermore it is the numbers within the smaller genera which produce this result. Amongst the larger genera the numbers present in each zone are very similar, a state of affairs inevitable owing to the fact that many of the larger genera occur in at least two if not all zones.

Among the smaller non-endemic genera those represented by one species only, i.e. monotypic, restricted to one endemic species or to one non-endemic species, are conspicuously fewer in the Temperate and Eremaean Zones than those in the 2–5 spp. group, but it will be noted in column (9) that the figures for the Tropical Zone are 360 and 320 respectively. It may be seen from columns (5), (7), and (13) that in the Temperate and Eremaean Zones it is the areas which share genera with the Tropical Zone that contribute many of the smaller non-endemics. Furthermore, when percentages for the total non-endemics are calculated it is seen that in the Temperate Zone 22·2, in the Eremaean 13·4, and in the Tropical Zone 40·2 per cent. fall in the single-species group. In other words, apart from the well-known richness of a tropical flora which would lead one to expect a high number of genera in the northern areas there is a significantly higher proportion of small genera in the Tropical Zone. These figures are, of course, subject to modification as the floras become better known.

Since no less than 239 (44+195) genera are represented in the Tropical Zone by a single species which is not confined to the Australian Region it seems worth considering whether a number of them are not migrants of comparatively recent arrival, especially in the case of those restricted, in their Australian occurrence, to the North-East Queensland area. While some occurrences may be due to the activities of man it is also probable that many are related to the last period of land communication with New Guinea during eustatic lowering of the ocean levels in the Pleistocene. On the other hand genera represented by a single endemic species doubtless include a number which are relict in nature and which date back to earlier periods when a tropical climate was more extensive.

Theoretically it is possible to divide small genera into three main types. Some are of recent origin, some of long standing but in which for one reason or another the rate of evolution is slow, and others are old genera or relict genera now reduced to a few species and sometimes to a restricted area. Unfortunately there are no adequate criteria by which these types may be recognized. Nevertheless a comparison between the number of endemics and non-endemics present in the Temperate Zone, column (1), and in particular those in the South-West Province, column (3), with those of the Tropical Zone, column (9), and those in North-East Queensland, column (11), gives the impression that in the southern areas the genera have had a longer history. That many of the genera of the Temperate Zone may represent ancient forms is substantiated by the fact that the proportion of endemic species is high in non-endemic genera (see figures in brackets), a state of affairs considered to indicate a long history within the zone. This proportion is higher than in the corresponding figures for the Tropical Zone while the non-endemic genera with endemic species only which are found in the Eremaean Zone are, with the exception of the 6–10 spp. group, always found either in the Temperate Zone also or are present in all Zones (see columns (6), (8), and (14)).

The general impression is that the Temperate Zone flora represents an older group, or at least includes a higher proportion of the descendants of early migrants and of early Australian endemics, than does that of the Tropical Zone. There is evidence, however, to show that the climate in southern Australia was warmer during certain stages of the Tertiary. Consequently it may be that the southern flora represents a residue from the early floras plus the taxa developed from forms which may no longer be present, but the tropical flora is a more complex one in which the existence of elements from the early floras has been partially obscured by numerous and more recent arrivals.

The origin of the flora of the Eremaea is of particular interest and will be discussed again in later parts of this paper. The general representation can be seen by considering columns (6), (8), (13), (15), and (16) in Tables 2 and 3 and may be summed up by saying that the majority of the endemics have southern or temperate affinities while the majority of the non-endemic genera are related to genera of the Tropical Zone. It should also be noted that there are a number of restricted endemics and also 16 non-endemic genera which are not recorded for either the Temperate or the Tropical Zone. These restricted genera, endemic and non-endemic, can be analysed as follows:

	Endemic	*Non-Endemic*
Gramineae	5	3
Cyperaceae		1

	Endemic	*Non-Endemic*
Santalaceae	1	
Loranthaceae		1
Chenopodiaceae	15	2
Amaranthaceae	1	
Aizoaceae	2	2
Capparidaceae	1	
Cruciferae	12	
Leguminosae	3	1
Stackhousiaceae	1	
Sapindaceae	1	
Bombacaceae	1	
Sterculiaceae	2	
Violaceae	1	
Myrtaceae	2	
Umbelliferae	2	
Apocynaceae	1	
Asclepiadaceae		2
Boraginaceae	3	1
Verbenaceae	4	
Labiatae	1	
Solanaceae	2	1
Pedaliaceae	1	
Acanthaceae	2	
Cucurbitaceae		1
Goodeniaceae	1	
Compositae	20	1

The series of families in this list shows no obvious relationship with those of either the Temperate or Tropical Zones since the emphasis is entirely different.

During the Cretaceous much of Central Australia was inundated by marine invasions and the continent was virtually divided into two or three islands with a resultant destruction of much of whatever vegetation there may have been. Following the retreat of these seas, i.e. in the Eocene–Miocene, the climate appears to have been subtropical, and rainfall was higher throughout the continent judging by the widespread development of a rain-forest type of vegetation. Judging by the fossil record (Duigan 1951) many tropical genera extended much further south than they would today but many typical "Australian" elements were already present. Nothing in this record suggests conditions under which genera tolerant of arid conditions would have found extensive habitats in which to develop. Were the ancestors of the present Eremaean flora present at that time or did they reach Australia at a later period? According to the geological record it may have been possible for land migrations between Asian areas and Australia to have occurred up until the Cretaceous but after this the contact was broken. Whether it is necessary to consider that this was entirely so is obscure since presumably it may have been possible for some invaders to cross the narrow seas to the north. Apart from these doubtful cases however the only definite communication would have been through New Guinea during the Pleistocene but as this was during the pluvial stage it too is not very promising.

The author is indebted to Dr. Smith White of Sydney for the suggestion that many of the Eremaean elements may have developed from species associated with coastal habitats. Such an opinion is supported by the prevalence of a number of genera which throughout the world are associated with coastal areas, sand dunes, or habitats of a saline type. Unfortunately the fossil record gives us almost no help but such an origin would indicate a pre-Tertiary arrival and a persistence in coastal areas until sometime in the middle Tertiary at least. However, once a seasonal climate with a winter rainfall system had been established then the probability of dry arid conditions in some area of inland Australia was greatly increased. It is proposed to discuss this problem further in the last part of this study, but at this stage it can be said that the Eremaean flora consists of elements which may have originally been temperate or tropical coastal types and these have been joined by temperate and tropical elements spread from the adjacent zones. It is this threefold nature of the Eremaean flora which gives it its special character.

As was mentioned earlier the present Eremaean Zone is crossed by the junction of the summer and winter rainfall systems. This junction is associated with certain vegetation and floristic changes. South of the junction one of the dominant grasses is *Stipa* and in the field the junction is marked by a change over to *Aristida*. In the south the Chenopodiaceae often dominate local communities, in the north these decrease sharply and similar habitats may be occupied by *Triodia* spp. Phyllodineous *Acacia* spp. occur throughout but they are particularly numerous in the northern section. Only in the north are the shrubby species of Tiliaceae conspicuous and in such places they tend to replace the species of Malvaceae which are common in the south. Nevertheless the differences appear gradually and there is no clearly definable boundary unless the *Stipa–Aristida* changeover is used.

Within the Tropical Zone a number of species are discontinuous in their occurrence (Specht 1958). These genera, all of which have strong Malaysian affinities, indicate that at a not too distant period the climate was wetter than that of the present day and hence a greater distribution would have been possible. That this was comparatively recent is indicated by the fact that the breaks are at the specific, not the generic, level and in all probability they had a more continuous development during one of the pluvial stages known to have existed during recent times. Similar discontinuities are found in eastern Australia, in North-East Queensland, the MacPherson–Macleay Overlap, and the Illawarra district of coastal New South Wales. It is suggested that these too may be associated with such climatic changes.

Taking such discontinuous occurrences together with the facts concerning distribution indicated in the tables it may be seen that Tropical genera can be grouped under those which have become widely diffused in Zones other than the Tropical one, those widespread in the Tropical Zone (subdivided into those in the open forest communities of the northern areas and those of the rain-forests and high rainfall areas of the east coast), those occupying disjunct areas, and finally those restricted to the North-East Queensland area. It seems probable that these groups are associated with different periods of arrival or of development within Australia during favourable climatic regimes. It is understood, of course, that such groups cannot be strictly defined owing to differing potential adaptabilities amongst the taxa involved. It is also possible that some of the most widely diffused forms need not have migrated from the tropical areas of the Near North but are survivals or rather the descendants of survivals from the warm climates of the early Tertiary and may therefore have migrated from the south rather than the north. Such forms may be, therefore, palaeoantarctic rather than palaeotropical.

In contrast to the situation in the north where geological records can be called on in support of views concerning migrations there is little indication of when and how arrivals may have come from the south. The only firm facts are those concerning distribution patterns and those relating to the scanty fossil records. Much has been written concerning affinities between the floras of South Africa and Australia. In the author's opinion these have been overemphasized with the result that the even closer links with the flora of South America have been too little heeded, though they have been better treated by Gardner (1944), Skottsberg (1953), and van Steenis (1953). It is remarkable how many genera occur in both these southern continents. Examples include *Orites*, *Eucryphia*, *Astelia*, *Nothofagus*, *Hebe*, *Oreomyrrhis*, and *Nicotiana*, to mention but a few. Incomplete though this list is it cannot be matched with one of genera common to Australia and South Africa where the affinities are mainly at the family or subfamily level rather than the generic.

The fossil record indicates that there were similarities between the plants of the early Tertiary in southern Australia and in South America but it should be remembered that these are plants developed under much warmer and wetter conditions than those current in southern Australia today. Consequently it is either among the elements of the "Australian" type or in suitable climatic niches in eastern or northern Australia that we should expect to find some indication of them since their descendants have either become adapted to present-day climates or they cling to areas with warm climates and an equable spread of rainfall. On the other hand there are affinities between the flora of Tasmania and New Zealand which are at the specific level, such as *Colobanthus apetalus* (coastal), *Oxalis lactea* (montane), *Pomaderris kumeraho*, *P. apetala* (low altitudes), *Acaena anserinifolia* (sea-level to 4000 ft), and *Myriophyllum propinquum* (aquatic). All of these are plants of cool climates and it is possible that they represent later migrants or developments in the Australian Region than do those represented in early Tertiary deposits. Nevertheless the occurrence of *Acaena anserinifolia* in New Guinea (Hoogland 1958) reveals a marked discontinuity in its distribution.

Since the distribution patterns both in the past and the present demonstrate the relationship between the floras of eastern Australia and South America, the importance of the former as a migration route over a very wide range of time is clearly indicated. As will be shown below there are a number of genera which occur over varying lengths of the route from South-East Asia to South America with divergences in some cases to New Caledonia and New Zealand. The two-way nature of movement along this route is suggested by the spread of such genera as

Eucalyptus, *Banksia*, *Lomandra*, and *Stackhousia* which either originated in the Australian Region or have produced the majority of present-day species within that area from whence they have now spread. The distribution patterns of these may be compared with those of *Orites*, *Nothofagus*, *Drimys*, and *Astelia* which appear to have had a southern origin, and with those of *Ficus*, *Elaeocarpus*, and *Tieghemopanax* which have affinities with the tropical floras.

Having considered the flora of the Australian Region as a whole it is now possible to discuss the representation in particular areas in the following sections before returning, in the final part of this account, to a further examination of the possible geological history of the Region since the Cretaceous and its relationship with the flora of adjacent countries.

B. FLORISTIC AREAS OF SPECIAL INTEREST AND IMPORTANCE

I. The South-West Province of Western Australia

The Province consists of that part of southern Western Australia which lies within the 10-in. isohyet. It impinges on the Eremaea in its northern section but to the east it is bounded by Interzone 1 into which a number of its characteristic genera and species extend but in which these are mixed with equally characteristic Eremaean elements (see Fig. 1).

The data concerning generic representation are analysed in Tables 4 and 5 in the same manner as in Tables 2 and 3. In Table 5 the terms "endemic" and "non-endemic" are used with reference to the Australian Region but the genera which are both endemic and restricted to the Province are shown in column (3) of Tables 4 and 5.

It is not possible to give details of the proportion of endemic species within all the various genera represented but it can be stated that the great majority of them are restricted to the Province or to the Province and Interzone 1 (western parts). As examples of genera whose species in the Province are restricted thereto the following may be quoted from the long list of possibles: *Thysanotus* (Liliaceae), *Lomandra* (Liliaceae or Xanthorrhoeaceae), *Oxylobium*, *Gastrolobium*, *Daviesia*, and *Pultenaea* (Leguminosae–Papilionaceae–Podalyrieae), *Boronia* (Rutaceae), *Cryptandra* (Rhamnaceae), *Thomasia* (Sterculiaceae), *Hibbertia* (Dilleniaceae), *Pimelea* (Thymelaeaceae), *Goodenia* and *Scaevola* (Goodeniaceae), *Stylidium* (Stylidiaceae), and *Helipterum* and *Helichrysum* (Compositae). It will be evident from these cases that though these genera, which occur in other parts of the Temperate Zone, make a substantial contribution to the total number of genera present in the Province the rate of endemism at the specific level is high over a wide range of families, i.e. over the whole range of the flora.

Among the families which Table 4 shows are well represented are the Restionaceae, Liliaceae (including Hutchinson's Xanthorrhoeaceae), Amaryllidaceae (including Hutchinson's Haemodoraceae–Conostyleae), Myrtaceae, Epacridaceae, and Goodeniaceae. The Province is the chief centre of development for the Tremandracae and the families Proteaceae, Leguminosae, Rutaceae, Rhamnaceae, and Verbenaceae are all well represented at the specific level (Gardner 1931). No less than six of the nine genera of the Pittosporaceae are present and of them two, *Pronaya* and *Sollya*, are restricted.

Though the Gramineae are represented by 25 genera they do not make any substantial contribution to the flora. Most of the genera are represented by one or few species though in *Stipa*, *Danthonia*, and *Poa* there are groups of species restricted to the Province. It is probable that the general paucity of the Gramineae results from the strictly winter incidence of the rainfall since only where summer rain or moisture is available do grasses make any conspicuous contribution to local plant communities.

Differing patterns of distribution are found amongst genera which, though represented to a greater or lesser degree in the Province, are also recorded for other parts of the Australian Region. It is proposed to discuss these under the following headings: (*a*) genera with suites of species in both the western and eastern parts of the Temperate Zone; (*b*) genera with the majority of species in the western part of the Zone; (*c*) genera with the majority of species in the eastern part of the Zone; (*d*) genera which are also widespread in the Eremaea; and (*e*) genera which have outlying species in the Tropical Zone.

(*a*) *Genera with Well-Developed Suites of Species in Both Western and Eastern Parts of the Temperate Zone*

Examples include *Lomandra*, *Xanthorrhoea* (both Liliaceae or Xanthorrhoeaceae), *Casuarina* (Casuarinaceae), *Persoonia* (Proteaceae), *Gompholobium*, *Daviesia*, *Pultenaea*, *Dillwynia*, *Hovea*, *Bossiaea* (Leguminosae–Papilionaceae), *Boronia*, *Eriostemon* (Rutaceae), *Spyridium* (Rhamnaceae), *Pimelea* (Thymeleaeaceae), *Commersonia* (Sterculiaceae), *Eucalyptus*, *Leptospermum*, *Melaleuca* (Myrtaceae–Leptospermoideae), *Leucopogon* (Epacridaceae), *Lobelia* (Campanulaceae), *Goodenia* (Goodeniaceae), *Olearia*, *Helichrysum*, *Helipterum* (Compositae).

Apart from these there is *Aphanopetalum*, the only member of the Cunoniaceae recorded for the Province. The genus is endemic to the Australian Region and there are only two species, one found in a restricted area near Geraldton in the South-West Province and one in coastal areas from south-east Queensland to eastern Victoria. It is possible that the family may have been more extensively developed in the west during the early Tertiary. *Xylomelum* (Proteaceae) shows a somewhat similar distribution with two species in the South-West Province and two in eastern Australia.

In the cases of *Lomandra*, *Casuarina*, *Daviesia*, *Pimelea*, *Melaleuca*, *Goodenia*, and the genera of Compositae the western and eastern groups are not entirely disjunct, even though most of the local species are restricted, since species of all are to be found in the intervening areas of the Eremaea and Temperate South Australia. Very few species, however, occur across the full distance.

In his study of the cytology of the Boronieae Smith White (1954*b*) expresses the opinion that the genera, such as *Boronia* and *Eriostemon*, which are found in both eastern and western centres, are pre-Miocene in origin. He further suggests

TABLE 4

NUMBERS OF GENERA REPRESENTED IN THE SOUTH-WEST PROVINCE, ARRANGED IN FAMILIES

SWP, South-West Province of Western Australia; *Temp*, Temperate Zone; *Trop*, Tropical Zone; *Er*, Eremaean Zone; *MMO*, MacPherson–Macleay Overlap

Family	*SWP* Total	*Temp* Residue	*SWP* Only	*Temp* + *Trop*	*Temp* + *Er*	*Temp* + *MMO*	All Zones
GYMNOSPERMS	4		1	2			1
MONOCOTYLEDONS							
Typhaceae	1			1			
Potamogetonaceae	5	2		1		1	1
Scheuchzeriaceae	1						1
Alismataceae	1						1
Hydrocharitaceae	3			3			
Gramineae	25	3	2	3	4	9	4
Cyperaceae	19	1	3	6		6	3
Lemnaceae	1					1	
Restionaceae	16	2	10	2		2	
Centrolepidaceae	4	1	1	1	1		
Xyridaceae	1			1			
Cartonemataceae	1			1			
Philydraceae	1		1				
Juncaceae	2					2	
Liliaceae	30	2	12	5	2	7	2
Haemodoraceae	1			1			
Amaryllidaceae	7	1	6				
Dioscoraeaceae	1			1			
Iridaceae	2		1			1	
Orchidaceae	21	1	4	4		12	
DICOTYLEDONS							
Casuarinaceae	1						1
Urticaceae	1						1
Proteaceae	15	2	4	3		4	2
Santalaceae	4				2	1	1
Olacaceae	1			1			
Loranthaceae	4		1				3
Rafflesiaceae	1		1				
Polygonaceae	2						2
Chenopodiaceae	12	1	3	1	5	1	1
Amaranthaceae	1						1
Gyrostemonaceae	3		1		2		
Aizoaceae	4	1			1	2	
Portulacaceae	1	1					
Caryophyllaceae	4	1			1	2	
Ranunculaceae	2					2	
Lauraceae	1			1			
Capparidaceae	1		1				
Cruciferae	5	2				3	
Droseraceae	1			1			
Byblidaceae	1			1			
Crassulaceae	1				1		
Cephalotaceae	1		1				
Saxifragaceae	1		1				
Pittosporaceae	6		2		1	3	
Cunoniaceae	1					1	

TABLE 4 (*Continued*)

Family	*SWP* Total	*Temp* Residue	*SWP* Only	*Temp* + *Trop*	*Temp* + *Er*	*Temp* + *MMO*	All Zones
Rosaceae	3	1	1			1	
Leguminosae	31	1	4	5	4	11	6
Geraniaceae	3				1	2	
Linaceae	1					1	
Zygophyllaceae	1				1		
Rutaceae	13	2	5	1		5	
Tremandraceae	3		2			1	
Polygalaceae	1				1		
Euphorbiaceae	9		2	1	1	4	1
Callitrichaceae	1					1	
Celastraceae	1		1				
Stackhousiaceae	1			1			
Sapindaceae	2				1		1
Rhamnaceae	6	2	1			3	
Vitaceae	1		1				
Malvaceae	3				3		
Sterculiaceae	5	2	2		1		
Dilleniaceae	1					1	
Guttiferae	1			1			
Elatinaceae	1			1			
Frankeniaceae	1				1		
Violaceae	1						1
Thymelaeaceae	1						1
Lythraceae	1					1	
Myrtaceae	26		13	3	3	4	3
Onagraceae	1					1	
Haloragaceae	4		1	1	1		1
Umbelliferae	9		2	1	2	3	1
Epacridaceae	15	1	7	3		4	
Primulaceae	1				1		
Oleaceae	1						1
Loganiaceae	2			1		1	
Gentianaceae	3			1		2	
Apocynaceae	2			2			
Convolvulaceae	7		1	1	1	1	3
Boraginaceae	2					1	1
Verbenaceae	5		3	1	1		
Labiatae	6	1	1		2	2	
Solanaceae	3				1		2
Scrophulariaceae	5				1	4	
Orobanchaceae	1	1					
Lentibulariaceae	2	1		1			
Myoporaceae	2				1		1
Plantaginaceae	1				1		
Rubiaceae	2					2	
Campanulaceae	5		1	1		1	2
Goodeniaceae	10	1	4	1	1		3
Brunoniaceae	1				1		
Stylidiaceae	2			1		1	
Compositae	30	2	3		17	4	4
Total	462	36	111	68	68	122	57

Table 5

NUMBER OF GENERA REPRESENTED IN THE SOUTH-WEST PROVINCE, ARRANGED ACCORDING TO ENDEMISM WITHIN THE AUSTRALIAN REGION AND NUMBER OF SPECIES

Numerals in parentheses indicate the number of genera with endemic species only

SWP, South-West Province of Western Australia; *Temp*, Temperate Zone; *Trop*, Tropical Zone; *Er*, Eremaean Zone; *MMO*, MacPherson–Macleay Overlap

Family	*SWP* (Total)	*Temp* Residue	*SWP* Only	*Temp* + *Trop*	*Temp* + *Er*	*Temp* + *MMO*	All Zones
Endemic genera							
Total	252	23	105	16	42	55	12
Monotypic	58	3	48	—	4	3	—
2–5 spp.	85	9	39	6	15	15	2
6–10 spp.	39	4	11	5	7	9	3
11–20 spp.	32	3	4	3	6	14	2
21–30 spp.	14	2	1	1	4	6	—
31–40 spp.	10	2	1	1	2	4	—
41–50 spp.	5	—	—	—	—	2	3
51–60 spp.	2	—	1	—	1	—	—
61–70 spp.	3	—	—	—	2	1	—
71–80 spp.	—	—	—	—	—	—	—
81–90 spp.	—	—	—	—	—	—	—
91–100 spp.	2	—	—	—	1	1	—
Over 100 spp.	2	—	—	—	—	—	2
Non-endemic genera							
Monotypic	2	—	1	—	—	1	—
Restricted to 1 endemic sp.	7	2	3	—	1	—	1
Restricted to 1 native sp.	14	1	—	6	1	4	2
2–5 spp.	65 (16)	10 (6)	2 (2)	12 (1)	7	29 (6)	4 (1)
6–10 spp.	31 (14)	—	—	6 (3)	4 (2)	13 (7)	8 (2)
11–20 spp.	30 (13)	—	—	10 (5)	3	8 (5)	9 (3)
21–30 spp.	12 (4)	—	—	5 (1)	2 (2)	3 (1)	2
31–40 spp.	13 (6)	—	—	4	3 (2)	3 (2)	3 (2)
41–50 spp.	7 (1)	—	—	2	1	1	3 (2)
51–60 spp.	7	—	—	2	3 (3)	—	2
61–70 spp.	5 (2)	—	—	1 (1)	—	2 (1)	2
71–80 spp.	6 (2)	—	—	2 (1)	1	1 (1)	2
81–90 spp.	1	—	—	—	—	—	1
91–100 spp.	3 (1)	—	—	—	—	2 (1)	1
Over 100 spp.	7 (3)	—	—	2 (2)	—	—	5 (1)
Total	462	36	111	68	68	122	57

that not only is a revision of the sections of *Boronia* required but that this would lead to an even greater emphasis on the differences between the western and eastern representatives.

The three Myrtaceous genera are all members of the Leptospermoideae and all are widespread in the Australian region. *Eucalyptus* is known from early Tertiary deposits (Duigan 1951) and probably all are of pre-Miocene origin. The cytology has been discussed by Smith White (1942, 1948*a*, 1948*b*). The tribe Beauforteae is restricted to the South-West Province, the Baeckeae have their main development in the Province, the Leptospermeae are more evenly divided between west and east, and the Eucalypteae include the widespread *Eucalyptus* and the purely eastern *Angophora*.

In his account of the cytology of the Chamelaucoideae Smith White (1950) lists twelve genera of which nine are either restricted to the South-West Province or have their chief development there. Those restricted to the east are small genera with few species. It is possible that further consideration of the generic circumscriptions may, in the future, lead to a separation of some of the eastern groups under distinct genera as has already been done in the case of *Agonis* (Leptospermoideae) formerly considered to have species in the South-West Province and others in south-east Queensland (Blake 1958).

The remaining tribe of the Leptospermoideae—the Metrosiderae—and the Myrtoideae differ in being not predominantly Australian and in not being represented in the Province. Both have strong tropical affinities and in Australia their distribution is either tropical or eastern.

It is thus evident that as far as the Myrtaceae are concerned those taxa present in the Province represent a very important assemblage phytogeographically. Since Smith White (1954*b*) considers the Chamelaucoideae may be less primitive than the Leptospermoideae there is little possibility that the area is one of origin rather than only one of development, but data are too scanty to indicate whether the Province should be regarded as a remnant of a former widespread assemblage or whether the flora was developed in this area and has migrated from it into other areas. Berry (1915) suggests that the Chamelaucieae are of "comparatively" recent origin, an idea which is in agreement with the fact that fossil pollens cannot be definitely assigned to this tribe (Cookson and Pike 1954) but further data are required before the significance of this latter fact can be understood.

With regard to the relative age of the flora in the Province it is interesting to find that there are striking differences in the amount of variability within species in the western and eastern parts of the Province itself which suggests that the flora of the western sections is a relict flora in some respects.

In both *Eucalyptus* and *Acacia* one of the features of the western sections is the comparative uniformity within the majority of species whereas the reverse is the case in the eastern sections. One of the most characteristic features of *Eucalyptus* in other parts of the Temperate Zone is the degree of variability shown within populations. Much of this has been due to hybridization or at least to the increased survival rate of hybrids following clearing operations. Brett (1946) has discussed this in relation to Tasmanian species and a number of studies on other species of eastern Australia have been made by Pryor (1953, 1955). Nevertheless, despite the fact that much of the land has been cleared in the South-West Province, confusion due to this cause is not a serious problem for the local botanist. The situation is completely changed in the lower rainfall areas of the Province, especially in sand plain or mallee heath country. This variability has been commented on by Gardner (1945) but it is essentially a feature of the natural communities rather than of the margins of cleared land. The result has been the description of a large number of species which may not be warranted though the confusion of forms present is not readily handled.

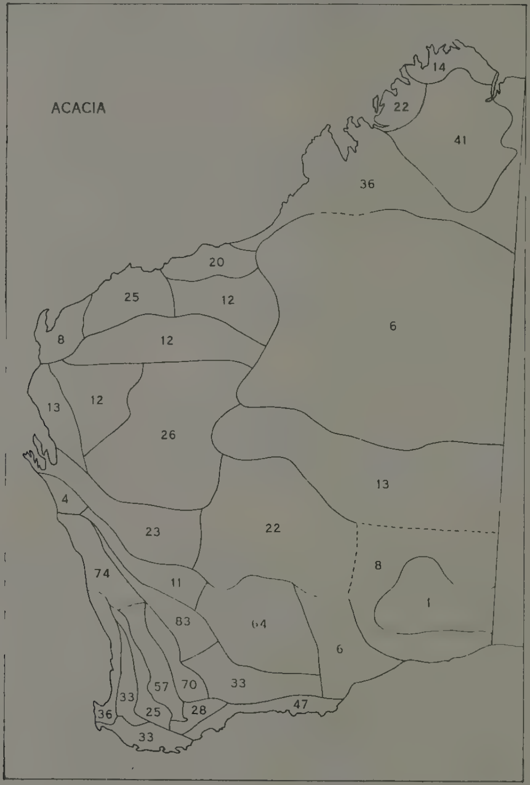

Fig. 2.—Number of species of *Acacia* recorded for different soil regions of Western Australia, showing high concentration in the Interzone 1 area. Based on Teakle's (1938) soil map and on specimens in the Western Australian State Herbarium.

There is a somewhat similar state of affairs in *Acacia* for which a large number of species have been described from the sandplains and from Interzone 1. Some of the species appear to form series over the range. An example is that of *Acacia acuminata* Benth. which is widespread in woodland communities receiving 15–20 in. of rain per annum. To the west it fails to penetrate far into the forested areas of higher rainfall but to the east it extends well into Interzone 1 where another species, very closely related, is recorded. This is *A. microneura* Meissn. and owing both to the close similarity and to the existence of what may be intermediates it is not easily separated though in the west the populations, despite some variation in phyllode length and width, are readily placed as *A. acuminata*. In the east, on the other hand, the populations become difficult to distinguish from *A. burkittii* F. Muell., a species of heavy soils or along water courses throughout the whole of the southern Eremaea east to New South Wales.

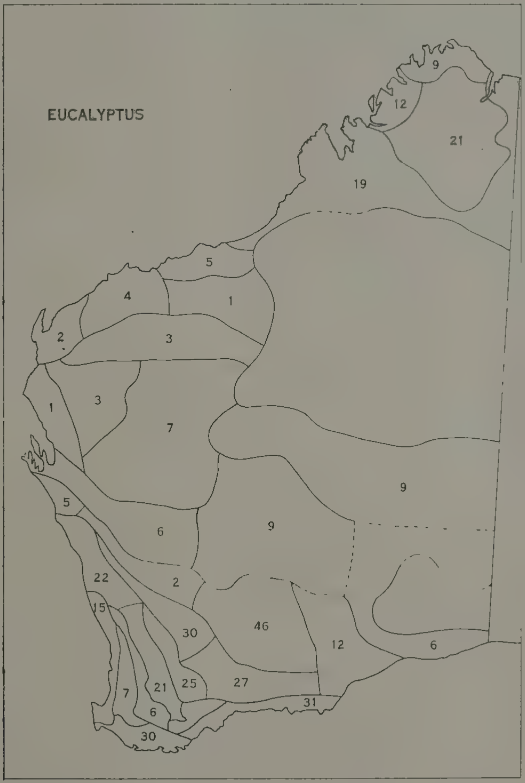

Fig. 3.—Number of species of *Eucalyptus* recorded for different soil regions of Western Australia, showing high concentration in the Interzone 1 area. Based on Teakle's (1938) soil map and on the records given in Blakely's (1934) key.

An attempt to demonstrate, even if only very approximately, the higher degree of variability within *Eucalyptus* and *Acacia* in the Province–Interzone 1 area was made by noting the number of "species" recorded for particular areas. The areas used are, for convenience sake, those of Teakle's soil map for Western Australia (1938). In the case of *Acacia* the figures are based on the specimens in the Western Australian State Herbarium, for *Eucalyptus* they are based on the records in Blakely's "Key to the Eucalypts" (1934). The results are shown in Figs. 2 and 3 and though the data are unsatisfactory in that they are biased by differences in collecting rates it is clear that there is a rise in the number of species along the boundary between the Province and Interzone 1. They also reveal a high number in the south coast areas. Of these latter the western half belongs to the Province proper and the species are well defined and restricted in their range. In the eastern part the number of species and the known variability agrees with the general pattern shown in the areas to the north of it.

It seems possible that the low degree of variability within the species of the western parts of the Province indicates that the area is a relic of a formerly much more extensive flora. This view is also in accordance with the relationships between west and east areas of the Temperate Zone and with the palaeoclimatic data. It also follows that a proportion of the species are themselves relict in nature since isolation and time appear to have combined to produce a certain uniformity within the populations. On the other hand the variability in the populations of the eastern section and in Interzone 1 may be explained by regarding them as a result of the climatic oscillations known to have occurred since the Pleistocene. These changes have resulted in both drier and wetter climates than that of the present and this must have involved a to and fro movement of the rainfall belts. The resulting conditions would have favoured Province and Eremaean forms alternately. It thus follows that many of the "species" may be of recent origin. It has also been suggested (Burbidge 1952) that this secondary area of speciation has seen the evolution of the mallee type in *Eucalyptus*.

Within the tribe Styphelieae of the Epacridaceae the genus *Leucopogon* is the largest and it is represented in the Province by at least 97 species (Gardner 1931) of which only three or four extend to South Australia. There is another group of species in eastern and south-eastern Australia and a few species are found outside the Australian Region. Smith White (1948*a*) suggests that the tribes Styphelieae and Epacrideae may have originated separately from the basic Ericales stock. Both tribes are well represented by restricted species within the Province. The Epacrideae include four genera, *Andersonia*, *Sphenotoma*, *Cosmelia*, and *Lysinema*, which are wholly restricted to the Province. An eastern species has been placed in *Lysinema* but it is probably better placed in the monotypic genus *Woollsia*. Smith White considers that the eastern epacrids represent an older group than do the western, a state of affairs possibly opposed to that found in the Myrtaceae and contrary to any view that the Province area is the point of origin of the "Australian" elements in the flora.

(*b*) *Genera with the Majority of Species in the Western Parts of the Temperate Zone*

These include *Thysanotus* (Liliaceae), *Patersonia* (Iridaceae), *Petrophila*, *Isopogon*, *Conospermum*, *Adenanthos*, *Banksia* (Proteaceae), *Gyrostemon* (Gyrostemonaceae), *Drosera* (Droseraceae), *Marianthus* (Pittosporaceae), *Oxylobium*, *Sphaerolobium*, *Aotus*, *Mirbelia*, *Kennedia* (Leguminosae–Papilionaceae), *Comesperma* (*Bredemeyera*) (Polygalaceae), *Tetratheca* (Tremandraceae), *Ricinocarpos* (Euphorbiaceae), *Cryptandra*, *Trymalium* (Rhamnaceae), *Rulingia*, *Thomasia*, *Lasiopetalum* (Sterculiaceae), *Hibbertia* (Dilleniaceae), *Baeckea*, *Calytrix*, *Darwinia* (Myrtaceae), *Logania* (Loganiaceae), *Anthocercis* (Solanaceae), *Scaevola*, *Dampiera* (Goodeniaceae), and *Stylidium* (Stylidiaceae).

It will be noticed that the genera of the Proteaceae, Leguminosae, and Myrtaceae are prominent in this list. Species of these often appear to dominate the local flora within the Province. It is also, so far as the genera in this list are concerned, a fact that though they are represented in the eastern parts of the Temperate Zone by a few species these are commonly either widespread or limited to a few disjunct localities. Widespread species include *Banksia marginata* Cav., *Oxylobium ellipticum* R. Br., *Sphaerolobium vimineum* Sm., *Kennedia prostrata* R. Br., *Ricinocarpos pinifolius* Dest., *Calytrix tetragona* Labill., *Dampiera stricta* R. Br., and *Stylidium serrulatum* Rich.

Cases of isolated occurrences probably should include some where recognition at the specific level of minor differences has separated what may be only geographic variants. This may be the case in *Trymalium*. Other cases include *Adenanthos terminalis* R. Br. and *Thomasia petalocalyx* F. Muell. where a single species extends the generic distribution to western Victoria. *Marianthus bignoniaceus* F. Muell. occurs in isolated areas in South Australia and in the Grampians in Victoria.

(*c*) *Genera with the Majority of Species in the Eastern Part of the Temperate Zone*

Examples include: *Danthonia* (Gramineae), *Ranunculus* (Ranunculaceae), *Correa* (Rutaceae), *Pomaderris* (Rhamnaceae), *Callistemon* (Myrtaceae), *Prostanthera* (Labiatae), *Veronica–Hebe* (Scrophulariaceae), *Galium* (Rubiaceae), *Wahlenbergia* (Campanulaceae), *Brachycome*, *Leptorrhynchos*, *Helichrysum* (especially subgenus *Ozothamnus*), *Craspedia*, and *Senecio* (Compositae).

It will be noted that the Proteaceae, Leguminosae, and Myrtaceae are not as important as in group (*b*) above. A number of the genera representing these families fall into groups (*a*) or (*b*) or they are restricted to the eastern part of the Temperate Zone. The list includes a number of herbaceous genera and there are more indications of affinities with regions other than the Australian one.

In recent treatments of *Brachycome* (Davis 1948) and *Swainsona* (Lee 1948) there is some evidence that development has proceeded at both the subgeneric and subspecific levels. In *Brachycome* the majority of the *Eubrachycome* are limited to eastern Australia whereas the majority of the *Metabrachycome* are in the South-West Province or in the Eremaea. Davis considers that the former is the more primitive group. In *Swainsona* the species are eastern and Eremaean but Lee recognizes subspecies in a number which have a wide distribution bringing them to the boundary of the Province. As in *Brachycome* the evidence suggests that the main centre is in the south-east of the Australian Region.

The species of *Craspedia* include the very widespread *C. uniflora* which is common in the South-West Province but, on present records, also common in the south-east Temperate areas including Tasmania. In the east, however, it shows much variation and forms have been recognized as distinct species by some of the earlier workers including Hooker (1856). Whether these variations represent "real" species or whether they are due to apomixis is not known but their existence serves to indicate the greater interest of the eastern forms.

In a recent paper on the subgenus *Ozothamnus* of *Helichrysum* it has been shown (Burbidge 1958) that there are two sections. In *Hebelaena* with seven species, two are confined to coastal areas of the South-West Province and the other five are associated with margins and clearings of monsoon forests in eastern and south-eastern Queensland and the MacPherson–Macleay Overlap. In section *Ozothamnus* there are 35 species, the majority in Tasmania and south-eastern Australia. One species is restricted to the MacDonnell Range in Central Australia and four, all restricted to small areas, extend west to Interzone 1 and the eastern parts of the Province. It is evident that here too the centre appears to be in the south-east.

(*d*) *Genera which are Important in the Eremaea as well as in the South-West Province*

These include: *Ptilotus* (Amaranthaceae), *Phebalium* (Rutaceae), *Phyllanthus* (Euphorbiaceae), *Dodonaea* (Sapindaceae), *Frankenia* (Frankeniaceae), *Micromyrtus*, *Thryptomene* (Myrtaceae), *Halgania* (Boraginaceae), *Eremophila* (Myoporaceae), *Newcastlia*, *Dicrastylis* (Verbenaceae), *Goodenia*, *Velleia* (Goodeniaceae), *Helipterum*, *Helichrysum*, *Podolepis*, *Myriocephalus*, *Angianthus*, *Gnephosis* (Compositae).

Most of the genera in this group are to be found in sand heath habitats of the northern and eastern parts of the South-West Province and in Interzone 1. In *Ptilotus* and the Compositae quoted the species are mostly annuals and hence members of the ephemeral flora. All of the genera decrease in importance and in representation in inverse proportion to the total rainfall. *Eremophila*, *Newcastlia*, and *Dicrastylis* exhibit their major development in the western Eremaea and in Interzone 1 but they, like the other genera mentioned, are widespread through the Eremaean Zone. It seems probable that they should be regarded as Eremaean elements which have diffused into the South-West Province (and also in some cases into other parts of the Temperate Zone) rather than temperate "Australian" elements in the narrower sense, i.e., they do not belong to the communities dominated by the sclerophyllous forms of Proteaceae, Myrtaceae, Leguminosae–Podalyrieae, and Epacridaceae.

(*e*) *Genera with Outlying Species in the Tropical Zone*

While the sharing of genera with the Eremaea is to be anticipated on geographical grounds and the correlation between western and eastern parts of the Temperate Zone is inevitable in the light of past climatic cycles, the occurrence in the Tropical Zone of isolated species of genera which are well developed in the South-West Province is not so readily explained. From a number of cases the following may be mentioned.

Borya (Liliaceae) has an extremely disjunct distribution. One species, *B. nitida* Labill., is common in the South-West Province but it is also recorded from the Grampians in Victoria. A second species, *B. subulata* C. A. Gardn., has been described from an isolated locality in the Kimberley (Tropical Zone), while a third species is restricted to North-East Queensland. Hutchinson (1934) places *Borya* in the tribe *Johnsonieae* for which the South-West Province appears to be the main centre. However *Laxmannia*, *Sowerbaea*, and *Tricoryne* also occur in eastern Australia and *Alania* is restricted to the Blue Mountains of New South Wales.

Under Hutchinson's arrangement of the Haemodoraceae (loc. cit.) the family includes nine genera which are distributed in Tropical America, South Africa, and Australia, there being two genera, *Phlebocarya* and *Haemodorum*, in the last-named region. The first of these is endemic and restricted to the South-West Province. The second is almost wholly restricted to the Australian Region with seven species restricted to the South-West Province, eight in the Tropical Zone and distributed from the Kimberleys to North-East Queensland (one species reaching New Guinea), two species in South-East Queensland and eastern New South Wales as far south as the Illawarra district though centred mainly in the MacPherson–Macleay Overlap and one outlier in Tasmania. The distribution is thus similar to that of the Corymbosae in *Eucalyptus* and may indicate a condition when warm climatic conditions extended further south than does the Tropical Zone at the present day or a condition when there was no Eremaean barrier to migration down the west coast of the continent.

Persoonia (Proteaceae), as has already been stated, has groups of species in both the western and eastern parts of the Temperate Zone. There is however also an outlier species, *P. falcata* R. Br. which is widespread throughout the Tropical Zone from the Kimberley to North-East Queensland. This is the only member of the Persoonioideae which occurs outside the Temperate Zone.

Byblis (Byblidaceae) is an Australian endemic represented by two species. One of these occurs only in the South-West Province and the other is widespread in the Tropical Zone. The only other genus of the family is South African.

Among the Leguminosae the following genera have species in the Tropical Zone: *Burtonia*, *Brachysema*, *Bossiaea*, *Jacksonia*, and *Mirbelia*. *Burtonia subulata* Benth. is widespread, *Brachysema* is represented by two or three species, *Bossiaea phylloclada* F. Muell. is also widespread as is *Mirbelia oxyclada* F. Muell. In a number of these the species extend to the northern parts of the Eremaea or the genera are also represented by Eremaean species, e.g. *Brachysema chambersii* (F. Muell.) Benth., or by species associated with refugia such as *Burtonia polyzyga* (F. Muell.) Benth. in the MacDonnell Range in Central Australia.

Jacksonia includes more than 30 species in the South-West Province; there are about nine species in the Tropical Zone of which three or four have been described from the Kimberley; and a further three or four extend into the northern Eremaea or down eastern Australia as far south as the north-east corner of Victoria. It thus has a distribution similar to that of *Haemodorum* and the Corymbosae in *Eucalyptus*.

Boronia (Rutaceae), though a characteristically southern genus, is represented by at least five species in the Tropical Zone. Geographically these seem to be discontinuous with the southern species, in both west and east, though the two suites approach each other in eastern Queensland.

Calytrix and *Verticordia* (Myrtaceae) are both very characteristic plants of sandy habitats in the South-West Province and it is in such areas that the majority of species are to be found. One species, *C. tetragona* Labill., is widespread in the eastern parts of the Temperate Zone and may include forms worthy of recognition at the specific level. A few species of *Calytrix* are found in scattered localities in the Eremaea and there are seven or eight species in the Tropical Zone. *Verticordia* is almost wholly confined to the South-West Province and Interzone 1. One species has been recorded for South Australia as *V. wilhelmi* F. Muell., but it is probably closer to the eastern *Homoranthus*. In the Tropical Zone the genus is represented by *V. cunninghamii* Schau. and by an undescribed species recorded by Specht (1958) for Arnhem Land. The reference to *V. grandis* Drumm. by Ewart and Davies (1917) must be regarded as requiring verification.

Diplopeltis (Sapindaceae) is represented by three species (sometimes reduced to one) in the South-West Province and by one species, *D. stuartii* F. Muell., which has been recorded for isolated localities in Central Australia, including the refugium of the MacDonnell Range, and also on the southern fringe of the Tropical Zone. The south-western species, or a variety of it, has also been recorded from Nichol Bay on the western extremity of the Tropical Zone.

The impression gained from all these distribution patterns is that despite the west–east affinities there are also affinities following an arc similar to but more extensive than that of the Tropical Zone. The northern relationships seem to be distinct from the west–east ones and it would be particularly interesting to know the basic relationships between the species involved and whether this distribution is a circumferential relationship or whether two distinct migration series are represented. It is obvious that the problem posed by these distributions is basic to the estimation of the South-West Province as a point of origin for the Australian elements in the flora of the Australian Region. The fact that the affinities are at the specific level makes it unlikely that the pattern dates back to floristic organization in the Tertiary.

Turning again to Table 5 the large number of endemic genera restricted to the Province is immediately evident since they make up 41 per cent. of the total. This further emphasizes the peculiar nature of the flora of the Province. It will be noted that there are seven genera, restricted to the area, which have more than ten species.

These are *Nemcia* (sometimes included in *Oxylobium*), *Beaufortia*, *Hypocalymma*, *Scholtzia* (all with 11–20 spp.); *Andersonia* (21–30 spp.); *Conostylis* (31–40 spp.?*); and *Dryandra* (51–60 spp.). Of these *Conostylis* represents the tribe Conostyleae which is restricted to this part of the Australian Region except for the genus *Lophiola* in North America—a distribution which appears to require further study. *Dryandra* represents the Proteaceae, *Andersonia* the Epacridaceae, and the remainder belong in the Leguminosae and Myrtaceae. It seems reasonable to suppose that these genera are of considerable antiquity. They are all members of the "Australian" element in the narrow sense and possibly some originated in this area of the Region. *Dryandra* is closely related to the widespread *Banksia*

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* The number of species in *Conostylis* may be reduced following the publication of work now in progress.

TABLE 6

NON-ENDEMIC GENERA OCCURRING IN THE SOUTH-WEST PROVINCE AND HAVING A WIDE DISTRIBUTION IN OTHER PARTS OF THE WORLD

Australian Distribution	Temperate Regions	Temperate and Subtropical Regions	Temperate–Tropical Regions	Tropical Regions	Cosmopolitan
Temperate Zones (including MacPherson–Macleay Overlap)	*Agropyrum* *Puccinellia* *Luzula* *Claytonia* *Sagina* *Hymenolobus* *Capsella* *Aphanes* *Glyceria* *Agrostis* *Deyeuxia* *Gyposphila* *Cardamine* *Epilobium* *Myosotis* *Mentha* *Veronica* *Euphrasia*	*Ruppia* *Linum* *Lythrum* *Sebaea* *Eryngium* *Orobanche**	*Calystegia* *Gratiola*		*Festuca* *Poa* *Lemna* *Juncus* *Salicornia* *Stellaria* *Clematis* *Ranunculus* *Rorippa* *Nasturtium* *Geranium* *Callitriche* *Apium* *Galium* *Cotula*
Temperate and Eremaean Zones	*Danthonia* *Erodium*	*Stipa* *Atriplex*	*Frankenia* *Arthrocnemum*		*Plantago* *Senecio* *Drymaria*†
Temperate and Tropical Zones	*Hypericum* *Centaurium*	*Cymodocea* *Avicennia*	*Typha* *Vallisneria* *Cladium* *Drosera* *Elatine* *Hydrocotyle* *Utricularia* *Lobelia*	*Dioscorea*	*Cynodon* *Carex* *Suaeda* *Myriophyllum* *Dichondra*
All Zones		*Cynoglossum*	*Aristida* *Eragrostis* *Cyperus* *Parietaria* *Acacia* *Phyllanthus* *Dodonaea* *Hybanthus* *Solanum* *Cuscuta* *Helichrysum*	*Jasminum* *Cressa* *Bonamia*	*Potamogeton* *Triglochin* *Scripus* *Eleocharis* *Polygonum* *Gnaphalium*

* Doubtfully native. † Mostly American.

TABLE 7

NON-ENDEMIC GENERA OCCURRING IN THE SOUTH-WEST PROVINCE AND SHOWING DISTRIBUTION PATTERNS INVOLVING ADJACENT REGIONS

* Genera with major centre in Australian Region; ** with large group of species in the South-West Province; † New Guinea; ‡ New Caledonia

Australian Distribution	Asia to Australia	Asia to SW. Pacific and New Zealand	Asia to South America	Australia to New Guinea and/or New Caledonia	Australia to New Zealand	Australia to South America	Australia to Africa	Southern Hemisphere
Temperate Zone (including MacPherson–Macleay Overlap)	***Patersonia* *Posidonia* (Mediterranean)	*Lepyrodia* *Corybas* *Cryptostylis* *Gastrodia* **Microtis* ***Caladenia* **Baeckea*	*Pratia* *Lagenophora*	**Caustis* **Eriostemon*	*Dichelachne* **Echinopogon*† *Microlaena*† *Calorophus* *Arthropodium*†‡ **Diuris* **Caleana* *Calochilus*‡ *Lyperanthus*‡ **Prasophyllum*‡ *Neopreissia* **Phebalium* **Poranthera* **Pomaderris*	*Amphibromus* *Hebe* *Polypompholyx* *Selliera* *Microseria*	*Tetraria* (N.Z.) *Spiloxene*(?) *Caesia*† *Carpobrotus*(?) *Pelargonium* ***Hibbertia* (Madagascar) *Villarsia*	*Acaena* *Mimulus*
Temperate and Eremaean Zones	*Lavatera* *Nitraria* (Africa)	*Glossostigma* **Calotis*			**Rhagodia* **Plagianthus* **Actinotus*‡ **Brachycome*†‡ *Craspedia* **Olearia*†		*Bulbine*(?) *Crassula* (N.Z.) **Rulingia* (Madagascar) *Athrixia* **Helipterum*	*Tetragonia* *Samolus*

TABLE 7 (*Continued*)

Australian Distribution	Asia to Australia	Asia to SW. Pacific and New Zealand	Asia to South America	Australia to New Guinea and/or New Caledonia	Australia to New Zealand	Australia to South America	Australia to Africa	Southern Hemisphere
Temperate and Tropical Zones	**_Stylidium_ _Hemarthria_ (Africa)	_Spinifex_ *_Schoenus_ **_Lepidosperma_ _Gahnia_ *_Centrolepis_ *_Dianella_ **_Thelymitra_ _Cassytha_ _Albizia_ **_Stackhousia_ *_Leptospermum_ **_Leucopogon_ _Trochocarpa_ *_Mitrasacme_ _Alyxia_ (Madagascar) _Parsonsia_	_Podocarpus_ (Africa) _Ottelia_ (Africa) _Carpha_ *_Leptocarpus_ (Africa)	*_Lomandra_ **_Haemodorum_ **_Banksia_ _Olax_ *_Hardenbergia_ (i.e. _Vandasia_) *_Ricinocarpos_	*_Pterostylis_†‡ _Acianthus_ **_Persoonia_		_Restio_	_Halophila_ _Xyris_
All Zones	**_Thysanotus_ *_Ptilotus_ **_Eucalyptus_ _Themeda_ (Africa)	**_Casuarina_ *_Exocarpos_ **_Pimelea_ **_Melaleuca_ *_Trachymene_ *_Myoporum_ **_Scaevola_ _Amyema_ _Amylotheca_	_Muehlenbeckia_ _Centipeda_ _Laurentia_ (Mediterranean)	*_Callitris_ **_Grevillea_ (Celebes)	_Vittadinia_†‡	_Nicotiana_	_Damasonium_	*_Haloragis_ _Wahlenbergia_ (Asia)

but Cookson and Duigan (1950) after a study of the morphology and anatomy of the leaves of both living and fossil specimens came to the conclusion that such characters are inadequate for the separation of the two genera and that there was, therefore, no evidence that *Dryandra* had ever occurred outside the South-West Province since leaves in Victorian brown coal deposits, believed to be of Oligocene age, might as truly belong to *Banksia*.

Of "non-endemic" genera only six are restricted to the Province. These are *Wurmbea* (Liliaceae), *Orthrosanthus* (Iridaceae), *Pilostyles* (Rafflesiaceae), *Porana* (Convolvulaceae), *Grammatotheca* (Campanulaceae), and *Trichocline* (Compositae).

Wurmbea is recorded for tropical and southern Africa but there are three species restricted to the Province. *Orthrosanthus* is found in extratropical South America apart from the five species in the South-West Province. *Pilostyles* is represented by a single species parasitic on *Daviesia pectinata* Lindl. The remaining species are distributed from western Asia to South America. *Porana* has its main centre in tropical Asia but there are a few species in Africa. It is represented in the Province by *P. sericea* (Gaud.) F. Muell. *Grammatotheca* is an interesting case as it is represented by *G. bergiana* var. *bergiana* which is widespread in South Africa. The occurrence of a subspecific taxon suggests that it may not be native, especially as it was not collected until after settlements had been established near the localities from which it was originally obtained. *Trichocline* is the only representative of the tribe *Mutisieae* to occur in the Australian Region. The sole species was placed in a monotypic genus *Amblysperma* by Bentham in the *Flora Australiensis*.

The remaining non-endemic genera occurring in the South-West Province have been arranged in Tables 6 and 7. In Table 6, genera which have a wide distribution in various parts of the world and which, therefore, cannot be easily related to particular areas or migration routes have been grouped under their general climatic regions. It would doubtless be possible to relate the Australian representation of these to special areas or special routes but unfortunately adequate information is not available. As a generalization it may be pointed out that the majority occur in other temperate areas of the world. Few of the genera have a large group of Australian species and none has its major centre in the Australian Region. The majority of the genera are represented by less than ten species. It is unlikely that any has originated in the Australian Region.

In Table 7 the genera are analysed according to particular distribution patterns. Genera which have their major centre in the Australian Region are marked with an asterisk, those with a large group of species in the South-West Province are marked with two asterisks. It will be noted that these "Australian" genera are in the majority but that as a whole most of the genera in the table fall into one or other of the groups covering portion or all of the route between Asia–Malaysia–Australia (without or with occurrence in New Guinea and New Caledonia)–New Zealand–South America. Most of the genera which are also found in New Zealand also occur in New Guinea or in New Caledonia. Of the 14 genera in the column "Australia to Africa" several are doubtful cases and two belong to the genera found through the arc from Madagascar to New Caledonia and do not occur on the African mainland. Of the doubtful genera the inclusion of *Spiloxene* (*Ianthe*) is dependent on the placing of certain Australian species at present retained under *Hypoxis; Carpobrotus* may not be truly native in Australia; *Bulbine* is now retained only for South African species and the Australian species are transferred to an Australian endemic genus *Bulbinopsis.*

Since a large number of the genera in Table 7 have their chief centre or at least a major group of species in the Australian Region it can be postulated that a considerable number of them have probably originated in the Region or that the Region is a developmental centre for them. Consequently if the genera in Table 6 be regarded as migrants into the Region then a number of those in Table 7 must be classed as emigrants from the Region. Furthermore since the relationships Asia–Australia and Australia–South America are so marked, even in so isolated a flora as that of the Province, it follows that contact between the Australian Region and these areas must have occurred (though probably interruptedly) over a very long period of time. It is evident that the relationships with the New Zealand flora lie through New Guinea and New Caledonia, a fact which indicates that the floras of Australia and New Zealand should not be grouped as "Australasian" unless at least parts of eastern Malaysia are also included.

Another inference that may be drawn from the data in Table 7 is that there is little evidence that the Province has been a point of entry or exit for migrating floristic elements. The relationships with genera also represented in eastern Australia suggest that floristic exchange has probably mostly been between east and west but the distribution of such genera as *Haemodorum*, *Jacksonia*, *Persoonia*, *Diplopeltis*, and *Borya* in the Tropical Zone shows that possible interchange between the Province and the north, at least during warm climatic phases, must be kept in mind. The lack of affinities with southern Africa is most marked and there seems nothing to indicate that the relationship between this area and that of the Province has ever been other than indirect.

Some of the genera in the Province are doubtless representatives of early Tertiary elements. *Podocarpus* is represented by a single species, *Callitris* has several western species, the endemic *Actinostrobus* has one or two species, and *Banksia* has its main group of species in the Province. There is also the isolated species of *Aphanopetalum*. The Cunoniaceae to which it belongs are a southern hemisphere family which is represented in early Tertiary deposits from Tasmania to Queensland (Duigan 1951) but most of the modern Australian species are found in the Tropical Zone or eastern Australia apart from one in Tasmania. *Aphanopetalum* may, therefore, be regarded as a relict of a former southern distribution of the genus or as having a distribution comparable to that of *Haemodorum* and *Eucalyptus*–Corymbosae and hence basically related to a tropical rather than a temperate distribution. In the latter case another example would be *Astrotricha* (Araliaceae) of which there is one species restricted to the Hamersley Range, on the south-west boundary of the Tropical Zone, and a group of species in eastern Australia from Queensland to Victoria. The Hamersley Range area appears to be refugial in nature and it is rich in endemic species (Burbidge 1959). The floristics

TABLE 8

NUMBERS OF GENERA REPRESENTED IN TASMANIA ARRANGED IN FAMILIES

Temp, Temperate Zone; *Trop*, Tropical Zone; *Er*, Eremaean Zone; *MMO*, MacPherson–Macleay Overlap

Family	Tas. Total	*Temp* Residue	Tas. Only	*Temp* + *Trop*	*Temp* + *Er*	*Temp* + *MMO*	All Zones
GYMNOSPERMS	8	1	5	1			1
MONOCOTYLEDONS							
Typhaceae	1			1			
Potamogetonaceae	6	3		1		1	1
Scheuchzeriaceae	1						1
Alismataceae	1						1
Hydrocharitaceae	2			2			
Gramineae	27	7		5	3	10	2
Cyperaceae	15	2		6		4	3
Lemnaceae	1					1	
Restionaceae	5	1		2		2	
Centrolepidaceae	5	3	1	1			
Xyridaceae	1			1			
Juncaceae	2					2	
Liliaceae	21	4	1	4	2	9	1
Amaryllidaceae	3	1	1	1			
Iridaceae	3	1				2	
Burmaniaceae	1	1					
Orchidaceae	21	1		6		14	
DICOTYLEDONS							
Casuarinaceae	1						1
Fagaceae	1					1	
Urticaceae	3					2	1
Proteaceae	12		3	4		3	2
Santalaceae	3				1	1	1
Olacaceae	1			1			
Loranthaceae	1						1
Polygonaceae	2						2
Chenopodiaceae	9	2		1	5		1
Amaranthaceae	2						2
Gyrostemonaceae	1				1		
Aizoaceae	1				1		
Portulaceae	3	2			1		
Caryophyllaceae	5	2				3	
Ranunculaceae	5	1	1		1	2	
Winteraceae	1			1			
Monimiaceae	1					1	
Lauraceae	1			1			
Cruciferae	8	1	1		3	3	
Droseraceae	1			1			
Crassulaceae	1				1		
Saxifragaceae	3		1			2	
Pittosporaceae	4				1	2	1
Cunoniaceae	1		1				
Rosaceae	4	1		1		2	
Leguminosae	21			3	3	10	5
Geraniaceae	3				1	2	
Oxalidaceae	1	1					

TABLE 8 (*Continued*)

Family	Tas. Total	*Temp* Residue	Tas. Only	*Temp* + *Trop*	*Temp* + *Er*	*Temp* + *MMO*	All Zones
Linaceae	1					1	
Zygophyllaceae	1				1		
Rutaceae	6	1	1	1		3	
Tremandraceae	1					1	
Polygalaceae	2			1	1		
Euphorbiaceae	9			2		5	2
Callitrichaceae	1					1	
Stackhousiaceae	1			1			
Sapindaceae	1						1
Rhamnaceae	5	1				4	
Elaeocarpaceae	2			2			
Malvaceae	2				2		
Sterculiaceae	1	1					
Dilleniaceae	1					1	
Eucryphiaceae	1	1					
Guttiferae	1			1			
Elatinaceae	1			1			
Violaceae	1					1	
Thymelaeaceae	2		1				1
Lythraceae	1					1	
Myrtaceae	8			1	1	3	3
Onagraceae	2		1			1	
Haloragaceae	3		1	1			1
Araliaceae	1			1			
Umbelliferae	14	4		2	3	4	1
Ericaceae	2		1			1	
Epacridaceae	16	3	2	4		7	
Primulaceae	1				1		
Plumbaginaceae	1			1			
Oleaceae	1	1					
Loganiaceae	1			1			
Gentianaceae	6	1	1	1		2	1
Apocynaceae	2			2			
Convolvulaceae	5			1	1	1	2
Boraginaceae	2					1	1
Labiatae	6				2	4	
Solanaceae	1				1		
Scrophulariaceae	9		1		1	7	
Bignoniaceae	1						1
Lentibulariaceae	2	1		1			
Myoporaceae	1						1
Plantaginaceae	1				1		
Rubiaceae	4	2				2	
Caprifoliaceae	1					1	
Campanulaceae	4			1		1	2
Goodeniaceae	5	1			1		3
Brunoniaceae	1				1		
Stylidiaceae	3		2	1			
Compositae	32	6	2		14	6	4
Total	401	58	28	71	55	138	51

Table 9

NUMBER OF GENERA REPRESENTED IN TASMANIA, ARRANGED ACCORDING TO ENDEMISM WITHIN THE AUSTRALIAN REGION AND NUMBER OF SPECIES

Numerals in parentheses indicate the number of genera with endemic species only
Temp, Temperate Zone; *Trop*, Tropical Zone; *Er*, Eremaean Zone;
MMO, MacPherson–Macleay Overlap

Family	Tas. Total	*Temp* Residue	Tas. Only	*Temp* + *Trop*	*Temp* + *Er*	*Temp* + *MMO*	All Zones
Endemic genera							
Total	122	21	14	6	27	50	4
Monotypic	21	2	13	—	2	4	—
2–5 spp.	41	15	1	—	9	16	—
6–10 spp.	13	—	—	3	3	7	—
11–20 spp.	22	2	—	2	5	12	1
21–30 spp.	9	1	—	1	2	5	—
31–40 spp.	5	1	—	—	2	2	—
41–50 spp.	4	—	—	—	1	2	1
51–60 spp.	1	—	—	—	1	—	—
61–70 spp.	3	—	—	—	2	1	—
71–80 spp.	—	—	—	—	—	—	—
81–90 spp.	—	—	—	—	—	—	—
91–100 spp.	1	—	—	—	—	1	—
Over 100 spp.	2	—	—	—	—	—	2
Non-endemic genera							
Monotypic	5	2	1	—	—	2	—
Restricted to 1 endemic sp.	21	6	9	—	2	3	1
Restricted to 1 non-endemic sp.	25	5	2	8	2	7	1
2–5 spp.	91	22	2	17	6	38	6
	(28)	(14)	(2)	(5)		(8)	
6–10 spp.	43	2	—	9	5	16	11
	(19)			(6)	(2)	(9)	(2)
11–20 spp.	33	—	—	12	4	9	8
	(15)			(7)		(6)	(2)
21–30 spp.	13	—	—	5	2	3	3
	(4)			(1)	(2)	(1)	
31–40 spp.	15	—	—	4	3	4	4
	(7)					(3)	(2)
41–50 spp.	4	—	—	2	—	1	1
51–60 spp.	7	—	—	2	3	—	2
	(3)				(3)		
61–70 spp.	6	—	—	2	—	2	2
	(3)			(2)		(1)	
71–80 spp.	5	—	—	2	1	1	1
	(2)			(1)		(1)	
81–90 spp.	1	—	—	—	—	—	1
91–100 spp.	3	—	—	—	—	2	1
	(1)					(1)	
Over 100 spp.	7	—	—	2	—	—	5
	(3)			(2)			(1)
Total	401	58	28	71	55	138	51

of this area are important in relation to the possible interchange of elements between the Tropical Zone and the South-West Province and the effects that past climatic changes have had on the representation.

It is probable that more light will be thrown on the question of routes by which interchange may have occurred between west and east and between south-west and north by a study of the distribution patterns and cytotaxonomic affinities between species as opposed to the generic relationships discussed here. Comments at this level must await the compiling of further data.

II. Tasmania

The generic representation in Tasmania is shown in Tables 8 and 9 which are arranged as in earlier instances. It will be found that the restricted endemics make up only 7 per cent. of the total flora and even if the genera endemic to the Australian Region are added endemism only rises to 30 per cent. as compared with 23·7 and 54·6 per cent. respectively for the South-West Province. It is possible that the rate of endemism would be slightly higher if the Tasmanian "Province" was considered to include the more elevated areas in Victoria such as the Australian Alps. Among the genera which would then be added are *Thismia* (Burmanniaceae) and *Diplaspis* (Umbelliferae). There is also *Cyathodes* (Epacridaceae) which is otherwise limited to New Zealand. Nevertheless the claims of Tasmania to be considered a distinct Province must rest not on endemism but on the nature of the whole assemblage and the differences between it and the flora of the mainland.

At the family level the Tasmanian flora includes a number which are not represented in the South-West Province. These are Burmanniaceae (only recently recorded for Victoria on the mainland), Fagaceae, Winteraceae, Monimiaceae, Elaeocarpaceae, Eucryphiaceae, Araliaceae, Ericaceae, Plumbaginaceae, Bignoniaceae, and Caprifoliaceae. Of these the Burmanniaceae, Elaeocarpaceae, Araliaceae, and Bignoniaceae have their chief centres of distribution in the tropics. The Fagaceae, Winteraceae, Monimiaceae, and Ericaceae are southern hemisphere elements even though the particular genera, *Nothofagus*, *Drimys*, *Atherosperma*, and *Gaultheria* are found in Malaysia. *Eucryphia*, the sole genus of the Eucryphiaceae, is found in Tasmania, south-east Australia, and South America. The Plumbaginaceae are represented by the cosmopolitan *Limonium* and the Caprifoliaceae by a species of *Sambucus*. None of the families is represented by more than a few taxa.

At the specific level the flora includes a number of restricted endemics but, as with the genera, a large number of species also occur on the mainland. On the basis of a rough estimate from the now outdated "Tasmanian Flora" by Rodway (1903) about 20 per cent. are restricted to the island.

The restricted genera are as follows: *Athrotaxis*, *Diselma*, *Microcachrys* (Gymnospermae), *Hewardia* (Liliaceae), *Campynema* (Amaryllidaceae), *Agastachys*, *Bellendena*, *Cenarrhenes* (Proteaceae), *Tetracarpaea* (Saxifragaceae), *Anodopetalum* (Cunoniaceae), *Acradenia* (Rutaceae), *Prionotes* (Epacridaceae), *Nablonium*, *Pterygopappus* (Compositae). It may be significant that both the Myrtaceae and Leguminosae are absent from this list. Both families are represented in early Tertiary deposits in Tasmania though in the former case only by *Eucalyptus* (Duigan 1951).

This lack of endemic representatives when taken into consideration with the fact that the other two important Australian families Proteaceae and Epacridaceae are represented by endemic genera which are always associated with cool habitats suggests that absence of the Myrtaceae and Leguminosae at the endemic generic level is due to partial destruction of an early "Australian" type vegetation during the Pleistocene glaciation and that only certain suitably adapted taxa survived. It follows that if any of the early types survived the most likely habitats would have been on the low-lying areas exposed in Bass Straits during a low level of the oceans and such areas would have been in communication with similar vegetation types in Victoria. An alternative would be to suppose that Tasmania was revegetated from a Victorian centre but this is inconsistent with the fact that northern and eastern Tasmania were not covered by the ice sheets which were very limited in extent (Jennings and Banks 1958). It is more logical to suppose that the Australian elements which did survive occupied the north of the island and the Bass Straits area and as these were in communication with the mainland during the more severe eustatic phases, or broken into a series of islands during the less severe, there was little opportunity for the development of restricted endemics amongst the "Australian" or "autochthonian" elements.

Some of the most interesting affinities of the Tasmanian flora seem to be those with the flora of the tropics and of other parts of the southern hemisphere. In connection with the former relationship it is interesting to consider the genera which occur not only in Tasmania but also in the Tropical Zone. These (if the genera recorded for all Zones be omitted) number 71 and they can be grouped as follows:

(*a*) *Genera Recorded for Southern and Eastern Australia from the South-West Province to North Queensland*

Gymnospermae: *Podocarpus*
Typhaceae: *Typha*
Potamogetonaceae: *Cymodocea*
Gramineae: *Hemarthria*
Cyperaceae: *Carpha*, **Cladium*, *Gahnia*, **Lepidosperma*, *Carex*
Restionaceae: *Leptocarpus*, *Restio*
Liliaceae: *Tricoryne* (E), *Dianella*, **Lomandra* (Conostyleae)
Orchidaceae: **Acianthus*, **Thelymitra*, *Pterostylis*
Olacaceae: *Olax*
Lauraceae: **Cassytha*
Leguminosae: **Hardenbergia* (?), *Hovea* (E)
Guttiferae: *Hypericum*
Elatinaceae: *Elatine*
Euphorbiaceae: *Beyera* (E)
Myrtaceae: **Leptospermum*
Umbelliferae: *Hydrocotyle*
Epacridaceae: *Acrotriche* (E), **Trochocarpa*, **Leucopogon*
Convolvulaceae: *Dichondra*
Campanulaceae: *Lobelia*

Four of the above are Australian endemics (marked E), a further eleven are marked with an asterisk to indicate that their major centres are within the Australian Region. Excepting *Cladium* and *Cassytha* all of these latter genera occur over a part or all of the range from the Malaysian area through New Caledonia to New Zealand but in a number of cases affinities are through the northern sections rather than directly Tasmania–New Zealand. Whether *Hardenbergia* is an Australian endemic or whether it is considered to include the species transferred to *Vandasia* and hence extend to New Guinea is a matter of opinion. This species is also found in North-East Queensland but its inclusion in *Hardenbergia* gives the latter a disjunct distribution in Queensland.

Three genera extend from Asia through Australia and the south-west Pacific to South America. They are *Carpha*, *Podocarpus*, and *Leptocarpus*. Only *Restio* indicates any generic affinity with the flora of South Africa. The remaining genera are all widespread but there is no strong indication of a northern origin.

(*b*) *Genera Recorded Throughout the Whole Area of the Temperate and Tropical Zones*

Hydrocharitaceae: *Vallisneria*
Gramineae: *Cynodon*, *Spinifex*
Cyperaceae: **Schoenus*
Centrolepidaceae: *Centrolepis*
Proteaceae: **Banksia*, *Persoonia*
Chenopodiaceae: *Suaeda*
Droseraceae: *Drosera*
Euphorbiaceae: **Ricinocarpos*
Stackhousiaceae: *Stackhousia*
Haloragaceae: *Myriophyllum*
Loganiaceae: **Mitrasacme*
Gentianaceae: *Centaurium*
Apocynaceae: *Alyxia*, *Parsonsia*
Lentibulariaceae: *Utricularia*
Stylidiaceae: **Stylidium*

Eight of the above have their main centres in Australia; *Banksia*, *Persoonia*, and *Ricinocarpos* being limited to one non-Australian representative each in New Guinea, New Caledonia, and New Zealand or in parts of this range. *Spinifex*, *Alyxia*, and *Parsonsia* are distributed between Asia and New Zealand but the Tasmanian occurrences are limited to one species each. The remaining genera are widespread or cosmopolitan.

(*c*) *Genera Recorded for the Tropical Zone and Eastern Australia including Tasmania*

Gramineae: *Imperata*, *Phragmites*
Liliaceae: *Chlorophytum*
Amaryllidaceae (Hypoxidaceae): *Hypoxis* (excluding *Spiloxene*)
Orchidaceae: *Dipodium*, *Dendrobium*
Elaeocarpaceae: *Elaeocarpus*
Leguminosae: *Desmodium*
Polygalaceae: *Polygala*
Plumbaginaceae: *Limonium*

None of these genera has its major centre in the Australian Region, and most of the affinities are tropical or cosmopolitan. All are widespread though *Polygala* is exceptional in not being recorded for Polynesia or New Zealand. *Chlorophytum* and *Elaeocarpus* are found from tropical Africa to the south-west Pacific, the latter also occurring in Madagascar. The inclusion of *Hypoxis* in this group rather than the group under (*b*) is dependent on an opinion that the Australian species under this name may include two genera, one having a southern distribution and the other, *Hypoxis* s. s. (?), occurring in eastern Australia and extending from the Old World tropics.

(*d*) *Genera Recorded for Eastern Australia from North-East Queensland to Tasmania*

Orchidaceae:	*Sarcochilus*
Proteaceae:	*Lomatia*, *Orites*
Winteraceae:	*Drimys*
Rosaceae:	*Rubus*
Rutaceae:	*Zieria*
Elaeocarpaceae:	*Aristotelia*
Araliaceae:	*Tieghemopanax*
Umbelliferae:	*Centella*
Epacridaceae:	*Dracophyllum*

This group reveals a number of affinities with South America. *Drimys* occurs from Asia to South America, *Lomatia* and *Orites* are restricted to the Australian Region and South America. *Aristotelia* is a genus of the southern hemisphere with centres of development in Australia and New Zealand. *Dracophyllum* is also in New Zealand but the Australian representation is limited to three species in very localized areas. *Tieghemopanax* is also recorded for New Caledonia and its affinities lie with the tropics rather than the southern areas.

Turning to Table 9 it may be seen that there are 14 genera restricted to Tasmania but non-endemic to the Australian Region. They are:

Gymnospermae:	*Phyllocladus*, *Dacrydium*
Centrolepidaceae:	*Alepyrum*
Ranunculaceae:	*Anemone*
Cruciferae:	*Cheesemannia*
Thymelaeaceae:	*Drapetes*
Onagraceae:	*Boisduvalia*
Haloragaceae:	*Gunnera*
Ericaceae:	*Pernettya*
Epacridaceae:	*Archeria*
Gentianaceae:	*Liparophyllum*
Scrophulariaceae:	*Ourisia*
Stylidiaceae:	*Donatia*, *Phyllachne*

Of these *Alepyrum*, *Cheesemannia*, *Archeria*, and *Liparophyllum* are otherwise limited to New Zealand. *Dacrydium*, *Drapetes*, and *Phyllocladus* are found from south-east Asia to New Zealand or to South America and their absence from present-day floras of the mainland is peculiar. The same applies to *Gunnera* which is distributed in the tropics and subtropics of the southern hemisphere, especially Malaysia and the Pacific. *Donatia*, *Phyllachne*, and *Pernettya* occur in New Zealand and South America. *Boisduvalia* and *Ourisia* are both primarily America genera and the single Tasmanian species of *Anemone* is widely separated from any close relative.

It is probably significant that all these genera, few of which are represented by more than one species, occupy habitats at comparatively high altitudes, i.e. they live in subalpine or alpine situations. They could, therefore, represent elements which would have had no great difficulty in persisting during the Pleistocene glaciations. The fact that they are not represented in the Australian Alps could indicate that either the intervening areas formed an impassable ecological barrier or that they arrived in Tasmania from a southern source too late to reach the mainland. Since, however, both *Phyllocladus* and *Dacrydium* are represented in the early Tertiary deposits of the mainland it is clear that this generalization cannot be applied to all the examples, and it is probable that some allowance must be made for the possible effects of severe arid periods, such as that of the late Pleistocene. Nevertheless even when such allowances are made it remains remarkable that some of these genera are monotypic and only represented in Tasmania and New Zealand. At present there seems to be no adequate explanation for this unless there was some relatively "recent" contact between the two areas.

When the distribution of the above groups of genera is compared with that of the Tasmanian plant fossil records (Duigan 1951) it is found that despite the differences between the floras a number of the genera must have been present at an early stage in Tasmania. These include *Podocarpus*, *Athrotaxis*, *Elaeocarpus*, *Fagus* (*Nothofagus*?), *Eucalyptus*, *Banksia*, *Lomatia*, *Coprosma*, and representatives of the Apocynaceae, Boraginaceae, and Sapindaceae. It is also interesting to find that the fossil records include *Araucaria* and *Ceratopetalum* not now present, and that the fossil leaves of *Eucalyptus* suggest those of the Corymbosae, a section of the genus which is now mainly tropical in its distribution apart from a few species in the South-West Province and *E. gummifera* which alone of the eastern species extends to as far south as eastern Victoria.

To sum up the above remarks it may be said that while the data are not very substantial it would appear that of the genera with tropical affinities which do occur in Tasmania some have been in the Australian Region for a very long time, some which appear on present-day distribution to be tropical may have had a southern origin and some which are not otherwise represented in the Australian Region may have reached Tasmania via New Zealand or through some land mass not now in existence. Finally, of those non-endemic genera now represented only in Tasmania (within the Australian Region) some may have reached the Region later than those whose earliest occurrence was associated with the rain-forests and wet-climate vegetation of the early Tertiary.

It would also seem that the comparative lack of endemics within the Australian element may be due in part to the destruction of much of this type of plant association during the Pleistocene glaciation and cold pluvial phase. What remained of this association was probably in communication with similar plant associations in southern Victoria across the exposed land of Bass Strait so that there has been an inadequate period for the development of Tasmanian endemic genera within plant associations of this type.

III. North-East Queensland

The North-East Queensland area is considered here to consist of the eastern parts of Cape York Peninsula which receive a high rainfall. As indicated by Brass (1953) in his summary of the 1948 Cape York Expedition the rain-forest and monsoon forest development is discontinuous in this area but nevertheless the number of families, genera, and species which, so far as the Australian Region is concerned, are restricted to this part of the Tropical Zone is outstanding. It is probable that increased knowledge of the flora of northern Australia will reveal that some of these genera extend further to the west but it is not anticipated that such changes will involve an alteration of the generalization.

Unfortunately there is no detailed account of the flora of the area and this analysis has had to be based on scattered records in taxonomic and more general botanical papers. For this reason it is impossible to be definite concerning the boundaries of the area or even whether it should be increased to include a greater area of the Peninsula or, alternatively, a longer subcoastal strip southwards. The account is probably incomplete owing to the emphasis laid on rain-forest and monsoon forest types in the literature. Possibly data concerning species of drier habitats would reveal the occurrence of some with more temperate affinities especially from those recorded not only for Australia but also for the montane areas of Malaysia (van Steenis 1934*a*, 1934*b*, 1936) and New Guinea (Hoogland 1958). At present there appears to be a strong discontinuity in such temperate elements so far as this part of Queensland is concerned.

The general data are analysed in Tables 10 and 11 which are arranged as in previous cases. It will be seen that, as was previously pointed out under Table 2, no less than 20 families are limited to this area so far as the Australian Region is concerned. These families are:

*Triuridaceae
*Musaceae
*Balanophoraceae
*Balanopsidaceae
Austrobaileyaceae (endemic)
*Calycanthaceae
*Himantandraceae
*Nepenthaceae
*Podostemonaceae
Hamamelidaceae
*Connaraceae
*Malpighiaceae
*Dichapetalaceae
Corynocarpaceae
Irvingbaileyaceae (endemic)
*Cardiopteridaceae
Actinidiaceae
*Ochnaceae
*Theaceae
*Elaeagnaceae

Of these families the Austrobaileyaceae and Irvingbaileyaceae are wholly endemic and restricted. The Balanopsidaceae and Corynocarpaceae indicate affinities with the floras of New Caledonia and New Zealand and serve to emphasize the

TABLE 10

GENERA REPRESENTED IN NORTH-EAST QUEENSLAND ARRANGED IN FAMILIES

Temp, Temperate Zone; *Trop*, Tropical Zone; *Er*, Eremaean Zone;
MMO, MacPherson–Macleay Overlap

Family	NE. Qld. Total	*Trop* Residue	NE. Qld. Only	*Trop* + *Temp*	*Trop* + *Er*	*Trop* + *MMO*	All Zones
GYMNOSPERMS	6	3		2			1
MONOCOTYLEDONS							
Typhaceae	1			1			
Pandanaceae	2	1				1	
Potamogetonaceae	3	1		1			1
Najadaceae	1					1	
Aponogetonaceae	1					1	
Scheuchzeriaceae	1						1
Alismataceae	2			1			1
Butomaceae	1	1					
Hydrocharitaceae	6	1	1	4			
Triuridaceae	1		1				
Gramineae	68	17	12	6	9	13	11
Cyperaceae	23	3	5	7		4	4
Palmae	18	5	9		1	3	
Araceae	7	4	1			2	
Flagellariaceae	1					1	
Restionaceae	2			2			
Xyridaceae	1			1			
Eriocaulaceae	1						1
Commelinaceae	6		1	2	1	2	
Cartonemataceae	1	1					
Philydraceae	2			1		1	
Stemonaceae	1	1					
Liliaceae	14	2		9	1	1	1
Haemodoraceae	1			1			
Amaryllidaceae	3			1		2	
Taccaceae	1	1					
Dioscoreaceae	1			1			
Musaceae	1		1				
Zingiberaceae	7	1	5			1	
Burmanniaceae	1	1					
Orchidaceae	45	6	22	8		9	
DICOTYLEDONS							
Casuarinaceae	1						1
Piperaceae	2					2	
Balanopsidaceae	1		1				
Moraceae	4		1	1		2	
Ulmaceae	1					1	
Urticaceae	7	2	1			3	1
Proteaceae	21		10	4		5	2
Santalaceae	2		1				1
Opiliaceae	2	1	1				
Olacaceae	1	1					
Loranthaceae	6					3	3

TABLE 10 (*Continued*)

Family	NE. Qld. Total	*Trop* Residue	NE. Qld. Only	*Trop* + *Temp*	*Trop* + *Er*	*Trop* + *MMO*	All Zones
Balanophoraceae	1		1				
Aristolochiaceae	1					1	
Polygonaceae	2						2
Chenopodiaceae	3	1		1			1
Amaranthaceae	5	2	1			1	1
Nyctaginaceae	4	1		1	1	1	
Aizoaceae	1					1	
Portulacaceae	1		1				
Caryophyllaceae	1				1		
Nymphaeaceae	3	1				2	
Ceratophyllaceae	1					1	
Menispermaceae	8	3	4			1	
Winteraceae	1		1				
Austrobaileyaceae	1		1				
Calycanthaceae	1		1				
Annonaceae	8		4			4	
Himantandraceae	1		1				
Eupomatiaceae	1			1			
Myristacaceae	1	1					
Monimiaceae	8		4	2		2	
Lauraceae	7			1		6	
Hernandiaceae	3	2	1				
Capparidaceae	3		1		2		
Nepenthaceae	1		1				
Droseraceae	1			1			
Podostemonaceae	1		1				
Saxifragaceae	4			1		3	
Pittosporaceae	3					2	1
Cunoniaceae	8		3			5	
Davidsoniaceae	1					1	
Hamamelidaceae	2		2				
Rosaceae	3	1	1	1			
Connaraceae	2		2				
Leguminosae	63	22	15	4	4	12	6
Linaceae	1		1				
Erythroxylaceae	1	1					
Zygophyllaceae	1						1
Rutaceae	16	2	1	3	2	8	
Simaroubaceae	5	2	1			2	
Burseraceae	2	2					
Meliaceae	13	4	3	2		4	
Malpighiaceae	2		2				
Polygalaceae	3		1	1		1	
Dichapetalaceae	1		1				
Euphorbiaceae	31	5	8	2		14	2
Anacardiaceae	6	4	1			1	
Corynocarpaceae	1		1				
Aquifoliaceae	2	2					

TABLE 10 (*Continued*)

Family	NE. Qld. Total	*Trop* Residue	NE. Qld. Only	*Trop* + *Temp*	*Trop* + *Er*	*Trop* + *MMO*	All Zones
Celastraceae	11		6			5	
Hippocrateaceae	3	1	2				
Icacinaceae	4		3			1	
Irvingbaileyaceae	1		1				
Sapindaceae	18	2	4		1	10	1
Cardiopteridaceae	1		1				
Rhamnaceae	8	3	2	1	1	1	
Vitaceae	4	2		1		1	
Elaeocarpaceae	5		2	2		1	
Tiliaceae	3		1		1	1	
Malvaceae	5	3			2		
Bombacaceae	2	1			1		
Sterculiaceae	10	4	1		1	2	2
Dilleniaceae	2	1	1				
Actinidiaceae	1		1				
Ochnaceae	1		1				
Theaceae	1		1				
Guttiferae	4	1	3				
Elatinaceae	1			1			
Cochlospermaceae	1	1					
Violaceae	1		1				
Flacourtiaceae	5	1	3			1	
Passifloraceae	2	1				1	
Thymelaeaceae	4		1			2	1
Elaeagnaceae	1		1				
Lythraceae	1		1				
Sonneratiaceae	1	1					
Lecythidaceae	2	2					
Rhizophoraceae	4	2				2	
Alangiaceae	1					1	
Combretaceae	2	2					
Myrtaceae	12	4		2		4	2
Melastomaceae	5	2	2			1	
Onagraceae	2	1		1			
Haloragaceae	2			1			1
Araliaceae	9	3	4	1		1	
Umbelliferae	3		1	1			1
Ericaceae	2		2				
Epacridaceae	3			3			
Myrsinaceae	7	1	2	1		3	
Plumbaginaceae	3	1		1		1	
Sapotaceae	8	2	4			2	
Ebenaceae	1					1	
Symplocaceae	1					1	
Oleaceae	5	1	1	1		1	1
Loganiaceae	5	2	2	1			
Gentianaceae	2	1					1
Apocynaceae	9	1	2	2		4	

TABLE 10 (*Continued*)

Family	NE. Qld. Total	*Trop* Residue	NE. Qld. Only	*Trop* + *Temp*	*Trop* + *Er*	*Trop* + *MMO*	All Zones
Asclepiadaceae	10	3	2	1	2	2	
Convolvulaceae	15	4	4	1	3		3
Hydrophyllaceae	1	1					
Boraginaceae	5	3			1	1	
Verbenaceae	11	2	2	1	1	5	
Labiatae	9	4	3	1		1	
Solanaceae	3	1					2
Scrophulariaceae	15	6	1		2	6	
Bignoniaceae	4	1	3				
Gesneriaceae	4		4				
Lentibulariaceae	1			1			
Acanthaceae	11	8	1	1		1	
Myoporaceae	2				1		1
Rubiaceae	30	11	9	1	3	6	
Cucurbitaceae	9	5			3	1	
Campanulaceae	2						2
Goodeniaceae	5			1	1		3
Stylidiaceae	1			1			
Compositae	24	6	2	3	1	5	7
Totals	870	212	227	106	47	207	71

importance of the area in this particular regard, there being stronger affinities with these islands through the north-east parts of the Australian Region than there are between the floras of eastern Queensland and New South Wales and of New Zealand.

Other restricted taxa include *Bubbia* (Winteraceae), five out of seven of the genera of the Zingiberaceae occurring in the Region, the monotypic *Tenagocharis* (Butomaceae), and the monotypic *Ganophyllum* (Burseraceae) though *Canarium* s. l. and *Garuga* are recorded for other parts of the Tropical Zone. As was to be anticipated all these cases indicate strong affinities with the floras of Malaysia and the south-west Pacific.

When the non-endemic genera which are restricted to North-East Queensland are checked it is found that 18 of them belong to the families in the above list. These families are marked with an asterisk and it follows that, as will be readily seen by checking with Table 2, this means that they are the only representatives of the family in the Region. However as the Malpighiaceae are recorded for the early Tertiary (Duigan 1951) for localities in the area of the present MacPherson–Macleay Overlap it cannot be assumed that the limitation of these families to the North-East Queensland areas necessarily indicates either a recent arrival or that there have not been times in the past when they had a wider distribution. Nevertheless a probability remains that some of them are recent migrants.

In Table 11, it will be noted that the endemic genera restricted to North-East Queensland are all small and there is nothing like the spread of sizes that is found in the South-West Province. On the other hand there are, in contrast to both the South-West Province and Tasmania, numerous though locally small genera amongst the non-endemic representatives. In considering this it is necessary to remember that the area has probably never been isolated from the rest of the Australian Region in the way that either the Province or Tasmania have. Consequently there has been less opportunity to build up restricted endemic species since there has been no special bar to the spread of any that may have originated in the area. In fact since the area was continuous with southern New Guinea during considerable periods of the early Tertiary and was reunited with New Guinea during low ocean stages of the Pleistocene it is actually more isolated at the present time than it was in the past especially when it is recalled that the current climatic cycle is "arid", not "pluvial".

When the restricted endemic genera are grouped under their families the following is the result:

Gramineae (F):	*Pheidochloa, Micraira*
Palmae (F):	*Normanbya*
Orchidaceae:	*Mobilabium, Drymoanthes*
Proteaceae (F):	*Placospermum, Musgravea, Opisthiolepis, Hollandaea, Cardwellia, Carnarvonia, Austromuelleria, Buckinghamia, Darlingia*
Austrobaileyaceae:	*Austrobaileya*
Annonaceae:	*Haplostichanthus*
Monimiaceae (F):	*Tetrasynandra*
Hernandiaceae:	*Valvanthera*
Hamamelidaceae:	*Ostrearia, Neostrearia*
Meliaceae (F):	*Rhetinosperma*
Euphorbiaceae:	*Neoroepera, Hexaspermum*
Anacardiaceae:	*Blepharocarya*
Celastraceae (F):	*Hexaspora, Hypsophila*
Irvingbaileyaceae:	*Irvingbaileya*
Sapindaceae (F):	*Synima, Sarcotoechia*
Rhamnaceae (F):	*Schistocarpaea*
Elaeocarpaceae (F):	*Peripentadenia*
Flacourtiaceae:	*Baileyoxylon*
Thymelaeaceae:	*Oreodendron*
Araliaceae (F):	*Motherwellia*
Bignoniaceae:	*Haussmannianthes*
Rubiaceae (F):	*Abbottia* (= *Timonius*)

The families in the above list include a number (marked F) for which fossil remains have been recorded in Australia (Duigan 1951). Though such records cannot be regarded as a complete representation of the families which must have been represented in the Region during the early Tertiary it can be said that the majority

TABLE 11

NUMBER OF GENERA REPRESENTED IN NORTH-EAST QUEENSLAND, ARRANGED ACCORDING TO ENDEMISM WITHIN THE AUSTRALIAN REGION AND NUMBER OF SPECIES

Numerals in parentheses indicate the number of genera with endemic species only
Temp, Temperate Zone; *Trop*, Tropical Zone; *Er*, Eremaean Zone;
MMO, MacPherson–Macleay Overlap

	NE. Qld. Total	*Trop* Residue	NE. Qld. Only	*Trop* + *Temp*	*Trop* + *Er*	*Trop* + *MMO*	All Zones
Endemic genera							
Total	93	13	36	16	2	19	7
Monotypic	42	7	30	—	—	5	—
2–5 spp.	34	6	6	7	1	13	1
6–10 spp.	6	—	—	4	1	1	—
11–20 spp.	7	—	—	4	—	—	3
21–30 spp.	1	—	—	1	—	—	—
31–40 spp.	—	—	—	—	—	—	—
41–50 spp.	1	—	—	—	—	—	1
51–60 spp.	—	—	—	—	—	—	—
61–70 spp.	—	—	—	—	—	—	—
71–80 spp.	—	—	—	—	—	—	—
81–90 spp.	—	—	—	—	—	—	—
91–100 spp.	—	—	—	—	—	—	—
Over 100 spp.	2	—	—	—	—	—	2
Non-endemic genera							
Monotypic	33	15	10	4	—	4	—
Restricted to 1 endemic sp.	103	19	74	1	—	8	1
Restricted to 1 non-endemic sp.	170	54	76	8	3	26	3
2–5 spp.	277	95	30	35	12	100	5
	(96)	(26)	(17)	(10)	(5)	(37)	(1)
6–10 spp.	92	13	1	13	13	34	18
	(34)	(1)	(1)	(8)	(3)	(17)	(4)
11–20 spp.	49	2	—	13	10	13	11
	(17)			(6)	(2)	(5)	(4)
21–30 spp.	14	1	—	3	3	3	4
	(1)			(1)			
31–40 spp.	11	—	—	3	2	—	6
	(2)						(2)
41–50 spp.	7	—	—	2	2	—	3
	(1)						(1)
51–60 spp.	4	—	—	2	—	—	2
61–70 spp.	4	—	—	2	—	—	2
	(2)			(2)			
71–80 spp.	5	—	—	2	—	—	3
	(1)			(1)			
81–90 spp.	1	—	—	—	—	—	1
91–100 spp.	—	—	—	—	—	—	—
Over 100 spp.	7	—	—	2	—	—	5
	(3)			(2)			(1)
Total	870	212	227	106	47	207	71

of the families listed must have been in the Region for a very long time and consequently these restricted genera may include a number of relict genera though others may not have appeared until a later period. Occurrence in New Guinea would *ipso facto* indicate an origin prior to that of the last loss of contact (unless it could be demonstrated that the Australian occurrence was due to human agency) though it would not indicate the area of origin.

It is possible that such genera as *Nepenthes*, *Calycanthus*, *Connarus*, *Dichapetalum*, and *Rhododendron*, none of which is restricted, may be suspected as being recent arrivals while *Cocos*, *Borassus*, *Caryota*, and *Musa* might either be recent migrants or have been introduced by human agencies prior to European settlement. Further information concerning the foods of indigenous peoples would doubtless disclose other plants which might have been introduced by this means.

Within the flora all the main floristic elements of the Australian Region are present. Early Tertiary elements, including some which may have had an Antarctic origin, are present. *Bubbia* (Winteraceae) may be taken as an example of a possibly Antarctic element; southern hemisphere elements are represented by members of the Cunoniaceae, Monimiaceae, and Haloragaceae; Australian elements include the Proteaceae and Epacridaceae; and tropical elements, most of which are Malaysian, have been discussed above.

That such elements should be present is natural and many of them also occur in New Guinea. However, there are a number of genera with a discontinuous distribution worth commenting upon. As has been noted in the comments on the flora of Tasmania there are certain genera which also occur in New Guinea, Malaysia, or New Zealand but which are not known today from the Australian mainland. Some of these, such as *Phyllocladus* and *Dacrydium* are recorded as fossils in Australian Tertiary deposits but there is no such evidence concerning *Drapetes* and *Gunnera*. Such a deficiency in the records is of course only negative evidence but in view of the fact that there are Tasmanian affinities with New Zealand at the specific level some migration other than that through the Australian mainland must be retained as a possibility even though the lack of suitable habitats in North-East Queensland may be an important factor.

It has already been shown (see Table 7) that there are numerous links between the floras of Australia, New Guinea, New Caledonia, and New Zealand which indicate that North-East Queensland must have been an important point of entry and exit (see Fig. 4). This is further illustrated by the representation in North-East Queensland. Nevertheless there are indications that two more or less distinct migration "tracks" may be present. Along one of these elements have moved into and out of Australia and Malaysia (in a general sense). The other track leads from New Guinea to New Zealand and the genera concerned are either those which have their major development within Australia (see Table 7) or they are represented by one or few species restricted to North-East Queensland. If this reading of the facts as known is correct then it suggests that movement along this second track has mainly been from rather than into Australia. There is little, if any, evidence that Australia has gained an appreciable number of floristic elements from this route since in the majority of cases they could as readily have been gained from parts of eastern Malaysia.

In a detailed analysis of the montane flora of Malaysia van Steenis (1934*a*, 1934*b*, 1936) has related the presence of certain plants to three main migration routes which he has called the Sumatran, Luzon, and New Guinea tracks respectively.

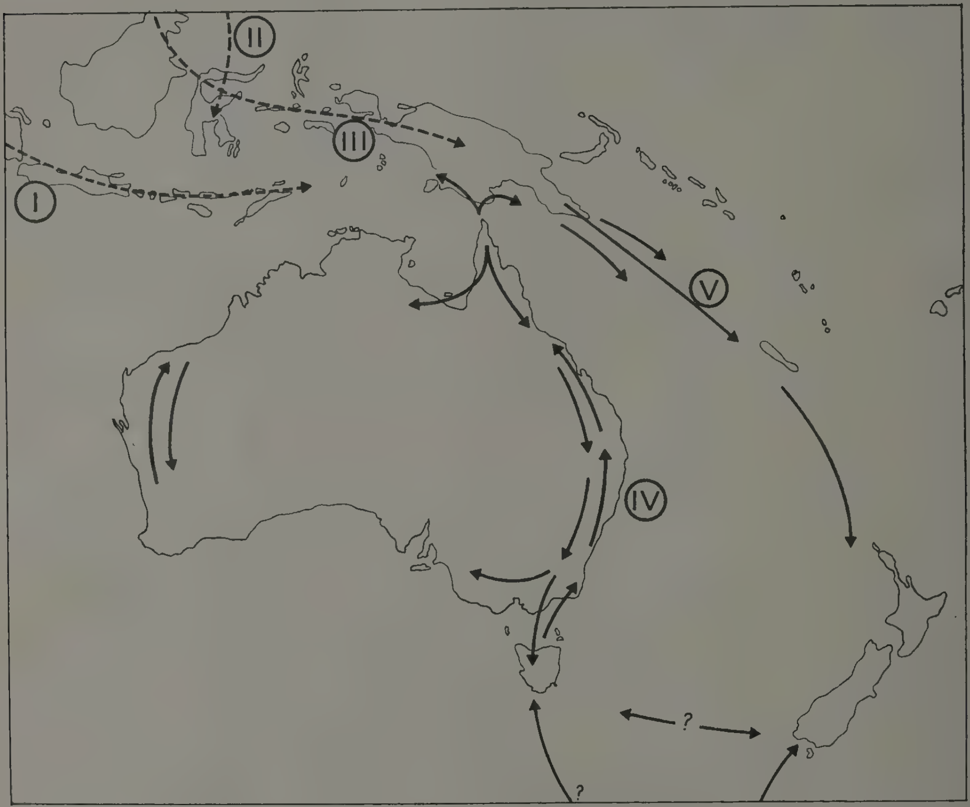


Fig. 4.—Migration tracks affecting the Australian Region. I, Sumatra track; II, Luzon track; III, New Guinea track; IV, Eastern Australian track; V, New Zealand track. Tracks I–III are based on van Steenis (1934*a*, 1934*b*, 1936). Movement within the Australian Region has undoubtedly been in more than one direction and there has been interchange with New Guinea.

He is particularly concerned with genera of temperate affinities and with the routes by which these could have penetrated the tropics. Since a number of the genera he discusses are also in the Australian Region, though few are recorded for North-East Queensland, his remarks have a special significance here. In his analysis of the elements of this type which have been recorded for the Lesser Sunda Islands he lists 81 phanerogams (species) of which 35 genera are also in the Australian Region. Of these 35, van Steenis refers 14 to the Sumatran track (plus two doubtful cases), eight (plus one doubtful) are referred to the New Guinea track, no opinion is expressed concerning a further eight and one is referred to both tracks.

Under the genera 15 species are also in Australia and of these three are referred to the New Guinea track and six are unreferred. With the exception of such genera as *Didiscus* (*Trachymene*), *Caladenia*, and *Microtis* which have their major centres in Australia and are particularly well represented in the South-West Province, the genera associated with the two tracks are mainly represented in eastern and south-eastern Australia. Thus though not all of the genera which are listed for both regions need to have migrated, in either a northward or a southward progress, via the North-East Queensland area the present distribution suggests that this was the most likely route. Furthermore Du Reitz (1931) considers that the contact between the northern and southern groups of species in *Euphrasia* has been through the "Malayan Bridge" (Fig. 8, p. 180). If this was so then migration could have been through North-East Queensland and south-eastern Australia or it could have been along van Steenis's New Guinea track to New Zealand to Tasmania and thence to Australia by some southern route. Since not all of the temperate elements discussed by van Steenis can have reached Australia by such a roundabout route it follows that the New Guinea track must have been divided into an Australian track following the more eastern parts of the Australian Region to Tasmania and another through New Caledonia and New Zealand from which there appear to have been some travellers which reached Tasmania without becoming established on the Australian mainland (see Fig. 4). This is consistent with the fact that 30 of the 35 genera are also in New Zealand and 21 have been recorded in New Caledonia.

The extensive spread of the genera along these tracks indicates that the migration must be a very old one. It does not seem possible to relate this movement to the cooler period of the Pleistocene alone though doubtless the elements made progress along certain parts of the routes at this time and it is possible that a number of the emigrations from Australia may have been as late as this. Van Steenis considers that the presence of these temperate elements in the Malaysian flora cannot be explained by supposing them to have entered during an Ice Age since there is no evidence that the life of the tropical vegetation has been interrupted by a cycle or cycles of less warm and humid conditions. It follows that the climate of North-East Queensland, also, must have been warm over the same period or one cannot explain the presence of so many tropical elements in this and in adjacent areas of northern and north-eastern Australia. Consequently the conditions under which temperate elements could have reached Australia from the northern hemisphere remain obscure despite the occurrence in the Region of such genera as *Euphrasia*, *Stellaria*, *Ranunculus*, *Drosera*, *Hydrocotyle*, *Centaurium*, *Mentha*, *Ajuga*, and *Viola*. The possibility of a southern point of entry and of emigration from Australia to Malaysia for some of these cannot be ignored but it would not cover all cases.

IV. The MacPherson–Macleay Overlap

As was explained in Part A the Tropical and Temperate Zones overlap in the eastern parts of their respective arcs (Fig. 1). The area concerned covers a corner of south-east Queensland and the high-rainfall areas of the North Coast of

New South Wales. Within this overlap tropical genera are found in the moister habitats of the wet gullies of the eastern slopes of the ranges while temperate genera occupy the more open habitats of the lower elevations or the higher slopes where temperatures fall below those suitable for the tropical species.

Although the area between the MacPherson Range and the Macleay River may be regarded as the main part of the Overlap it must be admitted that there is no very sharp demarcation, especially towards the south. Areas of Overlap associations have been described from the Barrington Tops by Fraser and Vickery (1937, 1938, 1939) and many of the genera which are well developed in the Overlap occur, in an increasingly discontinuous manner, south to the Illawarra district and the Shoalhaven River. Such southward extensions are linked with genera with tropical affinities or genera which require an equable climate with a high rainfall. Comparable occurrences of temperate genera to the north of the Overlap are uncommon and many of the temperate elements reach their northernmost localities within the Overlap. It is possible that so far as present-day conditions are concerned climate is a limiting factor, since in such northern habitats there is a marked winter drought and consequently temperate species are unable to make sufficient cool season growth to enable them to compete with tropical elements favoured by the summer rains. No such limitation affects the southern isolated communities of tropical genera since they are only found in sites on the eastern slopes of the ranges where the rainfall has comparatively even distribution throughout the year.

The general data are given in Tables 12 and 13. Two families—both monotypic—are restricted endemics. These are the Petermanniaceae and the Akaniaceae, *Petermannia* having been formerly placed under the Dioscoreaceae and *Akania* under the Sapindaceae. It is evident that both have tropical affinities. The list in Table 12 shows that further tropical affinities are numerous, e.g., genera in the Hydrocharitaceae, Philydraceae, Piperaceae, Ulmaceae, Moraceae, Urticaceae, Aristolochiaceae, Menispermaceae, Annonaceae, Lauraceae, Anacardiaceae, Celastraceae, Sapindaceae, Flacourtiaceae, Araliaceae, Myrsinaceae, Apocynaceae, and Asclepiadaceae apart from particular genera in other families with a wider world distribution.

In contrast to the importance of the tropical elements there are many "temperate" families but in few cases is there any substantial contribution to the generic representation. This applies to both "Australian" and "Antarctic" elements. Thus the Restionaceae are comparatively unimportant, the Liliaceae are represented by genera widespread through the rest of the Temperate Zone, there are no endemic restricted Proteaceae, Pittosporaceae, or Epacridaceae and the Leguminosae are mainly represented by genera with tropical rather than temperate affinities. The strong influence of tropical elements is also shown (see Table 12, column 3) by the number of genera which either extend south to the Overlap or are also found in the discontinuous communities further south. On the whole the situation suggests a marked advance of the tropical communities to a more southern latitude in the recent past, this advance having been followed by a retreat which has permitted reoccupation of certain areas by temperate communities but which has not been so catastrophic as to convert the temperate communities into highly competitive invaders, at least within the Overlap area.

In Table 13, 34 genera are listed as endemic and restricted. The majority of these belong to "tropical" families and most of them, as can be seen by consulting column (2) in Table 12, are single genera in a wide range of families. Only in the case of the Menispermaceae (3 endemics), Rutaceae (4 endemics), Orchidaceae (3 endemics), and Myrtaceae (2 endemics) is more than one genus involved.

Additional data concerning the representation within the Overlap can be gained from several ecological papers. Blake (1941) has given an account of the associations present in the vicinity of the Lower Stanley River in south-east Queensland, Fraser and Vickery have described in detail the vegetation of the Barrington Tops and Upper Williams River areas (1937, 1938, 1939) and more recently a list of species has been given by Baur (1957) in an account of the rain-forests of New South Wales. Blake divided his lists of species into those of the "closed forest" and "other communities". Fraser and Vickery treated their data under "subtropical rain-forest", "subantarctic rain-forest", and "eucalypt forest". Baur groups his list according to different rain-forest associations which in the table below have been combined into a single column. While there are differences between the results reported by these authors owing to basic differences in the ecological associations and to variations in the type of approach, the comparison between them, after minor changes in nomenclature, may be tabulated as in Table 14 in terms of genera representing various families.

Some of the differences between the communities are inevitably related to ecological rather than purely floristic factors. Thus there is an increase in the representation of the Gramineae, Leguminosae, and Compositae in the "open forest" communities in Queensland and in the eucalypt forests in New South Wales and this might be anticipated from the fact that the majority of such plants are favoured by strong light and inhibited by dense shade. However, a comparison of their representation in Table 14 with that in Table 12 shows that in the Gramineae and Leguminosae the effect of tropical elements is strong but that the temperate influence is evident in the Compositae.

The ecological studies also show that while the number of genera representing the families Proteaceae, Myrtaceae, and Epacridaceae, which are all important in the Australian Region, is low, there is an increase of Myrtaceae in the southern areas and this is paralleled by a corresponding increase in the number of species representing this family. Most of the Liliaceae are temperate genera but of the eight listed by Blake *Dianella*, *Lomandra*, *Arthropodium*, and *Caesia* are recorded for localities in Malaysia and New Caledonia; *Laxmannia* and *Xanthorrhoea* are represented by single species and are otherwise southern in their distribution; *Smilax* and *Ripogonum* appear to have tropical affinities though they occur from the Tropical Zone to eastern and southern Victoria; *Eustrephus* has been placed in the Philesiaceae by Hutchinson (1934) and has an Australian distribution similar to that of *Smilax* though the family is found in the southern hemisphere and *Cordyline* which has been transferred by Hutchinson to the Agavaceae is found only in eastern and north-east Queensland. Thus though the Liliaceae (in a broad

TABLE 12

GENERA REPRESENTED IN THE MACPHERSON–MACLEAY OVERLAP ARRANGED IN FAMILIES

MMO, MacPherson–Macleay Overlap; *Temp*, Temperate Zone; *Trop*, Tropical Zone; *Er*, Eremaean Zone

Family	*MMO* Total	*MMO* Only	*Trop* + *MMO*	*Temp* + *MMO*	*Trop* + *Temp*	*Trop* + *Er*	*Temp* + *Er*	All Zones	*Er* + *MMO*
GYMNOSPERMS	4		1		2			1	
MONOCOTYLEDONS									
Typhaceae	1				1				
Pandanaceae	1		1						
Sparganiaceae	1			1					
Potamogetonaceae	2			1				1	
Najadaceae	1		1						
Aponogetonaceae	1		1						
Scheuchzeriaceae	2	1						1	
Alismataceae	2				1			1	
Hydrocharitaceae	5	1			4				
Gramineae	69	4	16	12	9	11	4	12	1
Cyperaceae	24	1	5	6	8			4	
Palmae	4		3			1			
Araceae	3		2	1					
Lemnaceae	1			1					
Flagellariaceae	1		1						
Restionaceae	5	1		2	2				
Centrolepidaceae	1				1				
Xyridaceae	1				1				
Eriocaulaceae	1							1	
Commelinaceae	4		2		1	1			
Philydraceae	3	1	1		1				
Juncaceae	2			2					
Liliaceae	23	1	1	9	9		2	1	
Haemodoraceae	1				1				
Amaryllidaceae	5	1	2		1	1			
Dioscoreaceae	1				1				
Petermanniaceae	1	1							
Iridaceae	2			2					
Zingiberaceae	1		1						
Orchidaceae	38	4	10	16	8				
DICOTYLEDONS									
Casuarinaceae	1							1	
Piperaceae	2		2						
Fagaceae	1			1					
Ulmaceae	1		1						
Moraceae	4		2		1	1			
Urticaceae	7	1	3	2				1	
Proteaceae	17		5	5	5			2	
Santalaceae	6			3			2	1	
Olacaceae	1				1				
Loranthaceae	8		3	1				3	1
Aristolochiaceae	1		1						
Polygonaceae	2							2	

TABLE 12 (*Continued*)

Family	*MMO* Total	*MMO* Only	*Trop* + *MMO*	*Temp* + *MMO*	*Trop* + *Temp*	*Trop* + *Er*	*Temp* + *Er*	All Zones	*Er* + *MMO*
Chenopodiaceae	6			1	1		3	1	
Amaranthaceae	5	1	1			1		2	
Nyctaginaceae	3		1		1	1			
Phytolaccaceae	1		1						
Gyrostemonaceae	1						1		
Aizoaceae	5		1	2		1	1		
Portulacaceae	1						1		
Caryophyllaceae	3			3					
Nymphaeaceae	2		2						
Ceratophyllaceae	1		1						
Ranunculaceae	2			2					
Menispermaceae	6	4	1		1				
Winteraceae	1				1				
Annonaceae	5	1	4						
Eupomatiaceae	1				1				
Monimiaceae	7	2	2	1	2				
Lauraceae	7		6		1				
Capparidaceae	2					2			
Cruciferae	5			4			1		
Droseraceae	1				1				
Crassulaceae	1						1		
Saxifragaceae	7	1	3	2	1				
Pittosporaceae	7		2	3			1	1	
Cunoniaceae	8	1	5	2					
Davidsoniaceae	1		1						
Rosaceae	3			2	1				
Leguminosae	48		14	12	6	5	3	8	
Geraniaceae	3			2			1		
Linaceae	1			1					
Zygophyllaceae	1							1	
Rutaceae	22	4	8	5	3	2			
Simaroubaceae	3	1	2						
Meliaceae	7		4		2	1			
Tremandraceae	1			1					
Polygalaceae	3		1		1		1		
Euphorbiaceae	29	1	16	5	3		1	3	
Callitrichaceae	1			1					
Anacardiaceae	2	1	1						
Celastraceae	5		5						
Stackhousiaceae	1				1				
Icacinaceae	1		1						
Akaniaceae	1	1							
Sapindaceae	14	2	11					1	
Rhamnaceae	6		1	4	1				
Vitaceae	3	1	1		1				
Elaeocarpaceae	3		1		2				
Tiliaceae	3	1	1			1			
Malvaceae	6			1		4	1		
Sterculiaceae	8	1	2			2	1	2	
Dilleniaceae	1			1					

TABLE 12 (*Continued*)

Family	*MMO* Total	*MMO* Only	*Trop* + *MMO*	*Temp* + *MMO*	*Trop* + *Temp*	*Trop* + *Er*	*Temp* + *Er*	All Zones	*Er* + *MMO*
Guttiferae	1				1				
Elatinaceae	2				1	1			
Violaceae	2			1				1	
Flacourtiaceae	2	1	1						
Passifloraceae	1		1						
Thymelaeaceae	4	1	2					1	
Lythraceae	2			1		1			
Rhizophoraceae	2		2						
Alangiaceae	1		1						
Myrtaceae	20	2	4	7	2		2	3	
Melastomaceae	1		1						
Onagraceae	2			1	1				
Haloragaceae	2				1			1	
Araliaceae	4	1	1		2				
Umbelliferae	11			5	2		3	1	
Ericaceae	1			1					
Epacridaceae	12			9	3				
Myrsinaceae	4		3		1				
Primulaceae	2			1			1		
Plumbaginaceae	2		1		1				
Sapotaceae	3	1	2						
Ebenaceae	1		1						
Symplocaceae	1		1						
Oleaceae	3		1		1			1	
Loganiaceae	2			1	1				
Gentianaceae	4			2	1			1	
Apocynaceae	7		4		2	1			
Asclepiadaceae	6		2		1	2		1	
Convolvulaceae	8			1	1	3		3	
Boraginaceae	4		1	1		1		1	
Verbenaceae	10	1	6		1	2			
Labiatae	8		1	4	2		1		
Solanaceae	4						2	2	
Scrophulariaceae	16		6	7		2	1		
Bignoniaceae	1							1	
Gesneriaceae	1			1					
Lentibulariaceae	1				1				
Acanthaceae	3		1		1	1			
Myoporaceae	1							1	
Plantaginaceae	1						1		
Rubiaceae	13		6	3	1	2	1		
Caprifoliaceae	1			1					
Cucurbitaceae	4		1		1	2			
Campanulaceae	4			1	1			2	
Goodeniaceae	4						1	3	
Brunoniaceae	1						1		
Stylidiaceae	2			1	1				
Compositae	42	4	7	7	3	3	11	7	
Total	761	51	222	176	123	56	50	81	2

Table 13

NUMBER OF GENERA REPRESENTED IN THE MACPHERSON–MACLEAY OVERLAP, ARRANGED ACCORDING TO ENDEMISM WITHIN THE AUSTRALIAN REGION AND NUMBER OF SPECIES

Numerals in parentheses indicate the number of genera with endemic species only
MMO, MacPherson–Macleay Overlap; *Temp*, Temperate Zone; *Trop*, Tropical Zone; *Er*, Eremaean Zone

	MMO Total	*MMO* Only	*Trop* + *MMO*	*Temp* + *MMO*	*Trop* + *Temp*	*Trop* + *Er*	*Temp* + *Er*	All Zones	*Er* *MMO*
Endemic genera									
Total	191	34	23	76	19	6	23	10	—
Monotypic	50	28	7	11	—	1	3	—	—
2–5 spp.	64	6	15	27	7	3	4	2	—
6–10 spp.	25	—	1	10	5	2	6	1	—
11–20 spp.	25	—	—	14	5	—	4	2	—
21–30 spp.	11	—	—	6	2	—	2	1	—
31–40 spp.	4	—	—	4	—	—	—	—	—
41–50 spp.	5	—	—	2	—	—	1	2	—
51–60 spp.	1	—	—	—	—	—	1	—	—
61–70 spp.	3	—	—	1	—	—	2	—	—
71–80 spp.	—	—	—	—	—	—	—	—	—
81–90 spp.	—	—	—	—	—	—	—	—	—
91–100 spp.	1	—	—	1	—	—	—	—	—
Over 100 spp.	2	—	—	—	—	—	—	2	—
Non-endemic genera									
Monotypic	12	1	4	2	5	—	—	—	—
Restricted to 1 endemic sp.	27	9	10	5	1	—	1	1	—
Restricted to 1 non-endemic sp.	61	5	29	10	11	2	1	3	—
2–5 spp.	228	2	106	44	40	18	8	8	2
	(78)	(2)	(41)	(12)	(10)	(9)	(1)	(1)	(2)
6–10 spp.	100	—	34	16	13	14	4	19	—
	(43)		(17)	(8)	(9)	(3)	(1)	(5)	
11–20 spp.	65	—	13	10	15	10	4	13	—
	(30)		(5)	(7)	(8)	(2)	(4)	(4)	
21–30 spp.	20	—	3	3	5	2	3	4	—
	(9)			(1)	(1)	(2)	(3)	(2)	
31–40 spp.	18	—	—	4	4	2	2	6	—
	(6)			(3)			(1)	(2)	
41–50 spp.	8	—	—	1	2	2	—	3	—
	(1)							(1)	
51–60 spp.	7	—	—	—	2	—	3	2	—
	(3)						(3)		
61–70 spp.	6	—	—	2	2	—	—	2	—
	(3)			(1)	(2)				
71–80 spp.	6	—	—	—	2	—	1	3	—
	(2)				(1)		(1)		
81–90 spp.	2	—	—	1	—	—	—	1	—
91–100 spp.	3	—	—	2	—	—	—	1	—
	(1)			(1)					
Over 100 spp.	7	—	—	—	2	—	—	5	—
	(3)				(2)			(1)	
Total	761	51	222	176	123	56	50	81	2

TABLE 14

COMPARISON OF FAMILIES REPORTED FROM THE MACPHERSON–MACLEAY OVERLAP

CF, Closed forest; *OC*, other communities; *C*, common to communities in the area; *StF*, subtropical rain-forest; *SaF*, subantarctic rain-forest; *EF*, eucalypt forest

Family	Lower Stanley River, SE. Qld. (Blake 1941)			Barrington Tops and Upper Williams River, N.S.W. (Fraser and Vickery 1937, 1938, 1939)				Rain-forests (Baur 1957)
	CF	*OC*	*C*	*StF*	*SaF*	*EF*	*C*	
Gymnospermae	—	—	—	—	—	—	—	3
Typhaceae	—	1	—	—	—	—	—	—
Potamogetonaceae	—	1	—	—	—	1	—	—
Scheuchzeriaceae	—	1	—	—	—	—	—	—
Hydrocharitaceae	—	3	—	—	—	—	—	—
Gramineae	9	30	6	5	1	16	—	—
Cyperaceae	2	6	3	4	1	6	—	—
Palmae	1	—	—	—	—	—	—	3
Araceae	2	1	1	2	—	—	—	2
Flagellariaceae	1	—	—	—	—	—	—	1
Restionaceae	—	—	—	—	—	2	—	—
Commelinaceae	1	—	—	2	—	—	—	—
Juncaceae	—	1	—	1	—	2	—	—
Liliaceae	6	8	4	5	2	6	—	4
Dioscoreaceae	1	—	—	1	—	—	1	1
Petermanniaceae	—	—	—	—	—	—	—	1
Iridaceae	—	—	—	—	1	2	—	—
Zingiberaceae	1	—	—	—	—	—	—	1
Orchidaceae	2	5	2	8	1	12	—	1
Casuarinaceae	—	1	—	1	—	1	—	—
Piperaceae	—	—	—	2	—	—	1	1
Fagaceae	—	—	—	—	1	—	—	1
Ulmaceae	1	—	—	1	—	—	1	3
Moraceae	4	—	—	3	—	—	3	4
Urticaceae	2	—	—	3	3	—	1	1
Proteaceae	1	1	—	3	1	4	—	5
Santalaceae	1	1	1	—	—	2	—	—
Loranthaceae	1	1	1	1	—	1	1	—
Polygonaceae	—	2	—	—	—	—	—	—
Chenopodiaceae	2	—	—	—	—	—	—	—
Amaranthaceae	1	1	—	—	—	—	—	—
Phytolaccaceae	1	—	—	—	—	—	—	—
Gyrostemonaceae	1	—	—	—	—	—	—	—
Portulacaceae	—	1	—	—	—	1	—	—
Caryophyllaceae	—	—	—	1	1	2	—	—
Ranunculaceae	—	—	—	1	1	1	1	1
Ceratophyllaceae	—	1	—	—	—	—	—	—
Menispermaceae	1	—	—	2	—	—	2	2
Annonaceae	1	—	—	—	—	—	—	1
Eupomatiaceae	—	—	—	1	—	—	1	1
Monimiaceae	1	—	—	5	3	1	4	5
Winteraceae	—	—	—	1	1	1	1	1

TABLE 14 (*Continued*)

Family	Lower Stanley River, SE. Qld. (Blake 1941)			Barrington Tops and Upper Williams River, N.S.W. (Fraser and Vickery 1937, 1938, 1939)				Rain-forests (Baur 1957)
	CF	*OC*	*C*	*StF*	*SaF*	*EF*	*C*	
Lauraceae	—	—	—	3	—	—	3	5
Hernandiaceae	1	—	—	—	—	—	—	—
Capparidaceae	1	—	—	—	—	—	—	1
Cruciferae	—	—	—	—	1	1	—	—
Saxifragaceae	—	—	—	3	1	—	—	3
Crassulaceae	—	—	—	—	—	1	—	—
Pittosporaceae	2	—	—	4	2	2	—	4
Cunoniaceae	—	—	—	5	1	—	4	5
Rosaceae	—	—	—	2	2	2	—	—
Geraniaceae	—	—	—	—	—	1	—	—
Leguminosae	5	16	3	3	—	13	—	7
Oxalidaceae	—	1	—	—	—	—	—	—
Rutaceae	3	—	—	4	—	1	—	10
Simaroubaceae	1	—	—	—	—	—	—	—
Meliaceae	4	—	—	3	—	—	3	5
Polygalaceae	—	—	—	—	—	1	—	—
Euphorbiaceae	10	2	—	6	—	2	—	12
Anacardiaceae	2	—	—	1	—	—	1	2
Celastraceae	3	—	—	2	—	1	—	4
Icacinaceae	—	—	—	2	—	—	—	2
Sapindaceae	8	—	—	5	—	—	4	10
Akaniaceae	—	—	—	—	—	—	—	1
Rhamnaceae	1	1	1	2	—	—	1	1
Vitaceae	3	1	1	3	1	—	3	2
Elaeocarpaceae	—	—	—	2	1	—	2	2
Tiliaceae	—	1	—	—	—	—	—	—
Malvaceae	2	2	—	2	—	—	1	2
Sterculiaceae	1	1	1	2	—	—	1	2
Dilleniaceae	—	—	—	—	—	1	—	—
Guttiferae	—	—	—		—	1	—	—
Violaceae	—	1	—	—	1	2	—	—
Flacourtiaceae	1	—	—	1	1	—	—	1
Passifloraceae	1	—	—	1	—	—	—	—
Thymelaeaceae	1	—	—	1	—	1	1	—
Myrtaceae	3	6	—	9	—	8	—	5
Onagraceae	—	1	—	—	—	1	—	—
Haloragaceae	—	1	—	—	—	2	—	—
Araliaceae	1	—	—	3	—	2	—	—
Umbelliferae	—	—	—	1	—	4	—	—
Ericaceae	—	—	—	—	—	1	—	—
Epacridaceae	1	3	1	2	1	2	—	—
Myrsinaceae	1	—	—	2	—	1	—	2
Primulaceae	—	—	—	—	—	1	—	—
Plumbaginaceae	1	—	—	—	—	—	—	—

TABLE 14 (*Continued*)

Family	Lower Stanley River, SE. Qld. (Blake 1941)			Barrington Tops and Upper Williams River, N.S.W. (Fraser and Vickery 1937, 1938, 1939)				Rain-forests (Baur 1957)
	CF	*OC*	*C*	*StF*	*SaF*	*EF*	*C*	
Sapotaceae	3	—	—	1	—	—	1	2
Ebenaceae	2	—	—	1	—	—	1	1
Symplocaceae	1	—	—	1	—	—	—	—
Oleaceae	3	1	1	—	1	1	—	—
Gentianaceae	—	2	—	—	—	1	—	—
Loganiaceae	—	—	—	—	—	1	—	—
Apocynaceae	4	—	—	1	1	—	1	5
Asclepiadaceae	3	—	—	1	—	—	—	1
Convolvulaceae	—	—	—	1	—	1	—	—
Boraginaceae	—	—	—	2	—	1	—	1
Verbenaceae	2	2	1	2	—	—	1	3
Labiatae	1	2	1	1	—	5	—	—
Solanaceae	2	1	1	2	—	—	1	2
Scrophulariaceae	—	—	—	1	1	3	—	—
Bignoniaceae	1	—	—	1	—	1	1	1
Lentibulariaceae	—	—	—	—	—	1	—	—
Acanthaceae	1	1	1	—	—	1	—	—
Myoporaceae	—	1	—	—	—	—	—	—
Plantaginaceae	—	—	—	—	—	1	—	—
Rubiaceae	5	2	—	4	1	3	—	2
Caprifoliaceae	—	—	—	1	—	—	—	1
Cucurbitaceae	—	—	—	2	—	—	—	—
Campanulaceae	—	1	—	1	—	2	—	—
Goodeniaceae	1	1	1	—	—	3	—	—
Stylidiaceae	—	—	—	—	—	1	—	—
Compositae	—	7	—	2	—	15	—	1

sense) are mainly temperate this group of species demonstrates clearly the affinities which link the flora of the Overlap with that of Malaysia and other areas in the tropics.

Of the temperate genera listed by Blake the majority are approaching their northernmost limits so far as the Australian continent is concerned. These include *Poa*, *Microlaena* (both of which have been recorded for New Guinea), *Hardenbergia* (provided *Vandasia* which occurs in New Guinea be excluded), *Oxylobium*, and *Monotoca*. There is also a discontinuity between the southern species of *Persoonia* and *Persoonia falcata* of the northern Tropical Zone whose affinities lie with the species of the South-West Provice rather than with those of south-eastern and eastern Australia.

The Barrington Tops records are analysed in Table 15 to indicate the affinities of the genera.

The unlisted genera are *Aphanopetalum* of which there is one species in the Overlap and one in the South-West Province (see account of this area), *Howittia* which is centred in south-eastern Australia, *Commersonia* which is found in eastern Australia but is also in the Eremaean Zone, and *Astrotricha* which is an Australian endemic with 11 species, all of which are associated with the Dividing Range from Queensland to Victoria except for a single species limited to the Hamersley Range at the southern extremity of the Tropical Zone in Western Australia (see under South-West Province).

TABLE 15

ANALYSIS OF BARRINGTON TOPS GENERA

Subtropical Rain-forest			
Genera with tropical affinities			
Tropical Zone to Overlap	34		
Tropical Zone to Illawarra	36		
Tropical Zone to Victoria	19		
Tropical Zone to Tasmania	9		
		—98	
Genera restricted to the Overlap		5	
Widely distributed non-endemic genera		13	
Genera with temperate affinities		23	
Genera limited to eastern Australia within the Australian Region		9	
Unlisted		4	
			—152
Subantarctic Rain-forest			
Genera with temperate affinities		15	
Australian genera which extend to Tropical Zone		4	
Genera restricted to the Overlap		3	
Genera with tropical affinities			
Tropical Zone to Overlap or Illawarra		4	
Tropical Zone to Victoria		3	
Tropical Zone to Tasmania		4	
			—33
Eucalypt Forest			
Genera with tropical affinities		32	
Genera with temperate affinities		20	
Australian endemics (all southern or eastern in their distribution)		21	
Genera with a major developmental centre in the Australian Region			
(*a*) Asia to Australia, or Asia to New Zealand, or both		39	
(*b*) Australia to New Zealand		12	
Genera with a southern hemisphere distribution		9	
Cosmopolitan (mainly temperate)		21	
			—154

It will be noted that the subantarctic rain-forest is low in genera. This is probably due to the inhibiting effect of the dense shade on plants of the "Australian" element represented in the eucalypt forest and of the lower temperature on plants of tropical types. However, since the total assemblage of such adjacent associations in the Lamington Plateau area has been compared by Cookson and Duigan (1950) with the flora present in more southern areas during the early Tertiary, the poverty of the flora in the subantarctic rain-forest may be due to historical factors (i.e. it may be partially relict in nature) as well as to ecological and climatic factors of the present day.

Baur (1957) expresses the opinion that the pattern of rain-forest distribution in New South Wales with its marked discontinuities in the southern areas is due to a northward retreat as a result of the Pleistocene Ice Age and the subsequent periods of aridity. This does not appear to agree entirely with the data presented here since if the retreat now evident was basically due to a cooling of the climate one would expect to find more evidence of intrusion by temperate elements. Doubtless there was a retreat of the communities requiring warm conditions as a result of the cooling of the climate in the Pleistocene; but as coral formation was taking place on the Barrier Reef throughout the period or at least during the later phases (Browne 1945) the climate of Queensland cannot have been too cold for the development of coastal rain-forests. On the contrary, the interaction between cool land temperatures and warm seas would have meant a great increase in coastal fogs and the existence of conditions favourable for subantarctic type rain-forest if possibly less suitable for the more tropical associations.

The author considers that the discontinuities in rain-forest formation in New South Wales south of the Overlap are more likely to have resulted from climatic changes since and not during the Pleistocene. The pluvial stage of the Pleistocene was followed by a severe Arid Period but since then there seem to have been at least two pluvial periods, separated and followed by arid periods the last of which is still in progress. While the facts regarding these climatic changes and the respective intensities of the different stages are not altogether clear as yet it seems probable that there may have been at least two periods when the tropical rain-forest associations could have been extended southwards, since modern tolerances indicate that, provided the climate is both wet and not sharply divided into dry and wet seasons, rain-forests can advance considerably south of the Tropic. Each arid stage would have seen an arrest of this southward movement and a new retreat. As has already been said the present situation is one in which there has been a retreat of the communities rich in tropical elements and a reoccupation by temperate communities.

In a number of cases genera with Malaysian affinities have their southernmost occurrence in the Overlap area and in some of these there is a discontinuity in Queensland between the Overlap and North-East Queensland. This break in the distribution patterns is also shown in some Australian genera. Reference has already been made to the fact that the south-eastern Australian species of *Persoonia* do not advance far into eastern Queensland, the single northern species being related to those in the South-West Province. Another proteaceous genus which is discontinuous in this area is *Orites*, which has one outlying species in North-East Queensland and the remainder of the Australian species limited to the higher elevations from south-east Queensland to Tasmania. Other cases include *Endiandra*

(Lauraceae) which though not entirely disjunct has groups of species confined to either North-East Queensland or to the Overlap (Francis 1951); *Ceratopetalum* (Cunoniaceae) is discontinuous though it should perhaps be regarded as an Australian element and there is also a discontinuity in the Winteraceae between *Drimys* in the Overlap and in New Guinea and *Bubbia* in North-East Queensland. There are also a number of cases involving discontinuity between occurrence in the Overlap and in New Guinea. Examples include not only *Drimys* as quoted above but also *Acaena*, *Oreomyrrhis*, *Hebe*, and *Euphrasia* with which temperate elements the grasses *Poa* and *Danthonia* may be included (Hoogland 1958). There is also the case of *Arrhenechthites* quoted by Belcher (1956) as occurring in New Guinea and in the Blue Mountains of New South Wales.

Since these discontinuities concern plants with Malaysian affinities, Australian elements and also plants of subantarctic types it is clear that there can be no simple explanation based on a few climatic changes. Many of the distribution patterns must be of great antiquity and while they indicate that communities of tropical or temperate type must have undergone many transpositions north and south during geological times we have too little data to permit even a tentative history of their migrations.

The evidence presented here does not indicate that the MacPherson–Macleay Overlap has a flora of sufficient distinctiveness to make it a definite phytogeographic province but its composition shows that it is an area of the greatest importance in any discussion concerning plant migrations. There can be no doubt that eastern Australia, especially the floristic communities represented along the Dividing Range and the east coast, has been for a very long period one of the most important plant migration routes that may be traced between the northern hemisphere and subantarctic regions. For this reason alone it is worthy of special attention from the plant geographer.

C. THE FLORA OF THE AUSTRALIAN REGION IN RELATION TO ITS GEOLOGICAL HISTORY, GEOGRAPHICAL AFFINITIES, AND PROBABLE MIGRATION ROUTES

I. INTRODUCTION

It was Hooker (1856) who first drew attention to the relationships between genera of isolated land masses in the southern hemisphere and to the presence, in the Australian flora, of elements that could be referred to as "Antarctic". Since then the problems relating to plant distribution have been discussed in many papers but, so far as the Pacific area is concerned, we are still far from a generally acceptable or accepted explanation.

Among the more important hypotheses which have been advanced by various authors to explain relationships between the land areas of the world are the Wegenerian hypothesis of continental drift, the Gondwanaland hypothesis, the postulation of land bridges to cover gaps now occupied by oceans and finally the ideas of Croizat (1952) who lays particular emphasis on the importance of the southern Pacific as a point of origin for many angiosperm families even though the land area is now so small. At present workers seem to be divided into those who fully accept the Wegenerian hypothesis (usually with some of the modifications proposed by later authors) and those who believe in the essential stability of the continental masses. These two points of view must, owing to recent developments, be seen in the light of the data resulting from research in palaeomagnetism. The information concerning polar migrations, with or without associated continental movement, has obvious implications for every plant geographer.

If continental drift is to provide a satisfactory explanation of the affinities between the floras of the Australian Region and of other lands it should fulfil the following requirements: (i) the time scale should allow for suitable contacts during the major period of angiosperm development; (ii) drift must be able to explain incongruous and discontinuous distributions without creating difficulties in other cases; and (iii) there should be a climatological "fit" as well as a geographical one. In our present state of knowledge it would be difficult for any hypothesis to satisfy all these conditions. Without a clearer time scale it is difficult to assess the value (for the present purposes) of the scheme covering continental displacement put forward by Carey (1958) and, so far as the second point is concerned, the inadequacy of continental drift as a means of explaining plant distributions in the Pacific has been thoroughly discussed by Gordon (1949) and by Skottsberg (1956). The third point is linked with polar migrations but, since Irving (1958) writes with some reserve when correlating these with continental movements, their significance and their bearing on plant geographical problems in the southern hemisphere is not fully established.

The author's views may, therefore, be defined as an unwillingness to accept any hypothesis without reservation. Continental drift does not solve all the difficulties, especially within the available portion of the time scale. This does not imply that the importance of the relationships with the flora of other southern lands is denied. On the contrary the strong generic affinities with the flora of South America and, by contrast, the lack of generic affinities with Africa and India (except indirectly) represent a feature that the reconstructions of Pangaea (Carey 1958) fail to explain. Similarly the "tropical" elements of long standing in the Australian flora suggest that the region must have been in contact or communication with areas other than that of the Antarctic prior to the early Tertiary. These facts must be explained without forgetting that certain genera in the Australian flora are apparently related to those of certain temperate areas in the northern hemisphere. Attempts to correlate these facts with the movements proposed by those favouring continental drift result in complexities both geographical and climatological in nature. The plants are present but the fact that the paths by which they arrived remain obscure seems an unsatisfactory basis for accepting the drift hypothesis, especially when affinities with South Africa are so remote.

It is accepted as a principle that plant migration has been by advance and retreat of communities and not, at least in the great majority of cases, by chance arrivals. The migration of communities rather than of individuals has been discussed by Gordon (1949) and by Evans (1958). The latter author visualizes a community in terms not only of its plants but also of its associated insect fauna, a timely reminder that ecological balance is based on both zoological and botanical factors.

The best-known fossil floras of Australia are the early Tertiary assemblages commonly referred to as the "Cinnamomum flora". These assemblages have affinities with fossil floras of comparable age in other parts of the southern hemisphere, notably those of South America. Modern representatives of the fossil species are now to be found amongst the plants of New Guinea, New Caledonia, New Zealand, and South America and, to a much lesser extent, South Africa. When past and present distribution is considered it appears that this early floristic type existed during a period of warm climate and this assumption is supported by other palaeontological data. It follows that there has been either a northward migration or northward retreat of this flora. Migration seems the more likely in view of the relationships with South America and South Africa.

Certain assumptions are made for the purposes of this discussion. The first is that if a family or group of genera is limited to or has a distribution related to particular climatic conditions at the present time then it is probable that a similar relationship existed in the past. This concept is almost universally accepted in biogeographical and palaeontological discussions. Without it the position would be almost insurmountably complex.

The second assumption is that while small genera may be either "young", "old but not rich in species", or "relict", the large genera must be of considerable age and have occupied the major part of their present distribution range for a long period. The rate of production of species must have varied in different genera, quite apart from the differences related to the perennial or annual habit and the length of generations, but for comparative purposes this generalization seems justified.

Applying these assumptions it would seem that the flora of the early periods includes not only many which may be suspected as being of southern origin or from the Antarctic but also taxa of a tropical type. This, with the presence of Malaysian elements in the modern flora, indicates that the continent has been open to migration from the north for a very long period. Not only are tropical elements well distributed in the Region but the flora of the Eremaea includes a number of taxa related to temperate and arid area species of the northern hemisphere. It is suggested that these were originally strand and dune plants which reached Australia before or during the Cretaceous or in the early Tertiary. Their first development was possibly related to the extensive coastlines of the Cretaceous, their later to the arid periods of the Pleistocene and of more recent periods. Their migration and to some extent their assemblage is distinct from that of the Antarctic and Malaysian elements represented in the Temperate and Tropical Zones.

While there are many indications of affinities through the Antarctic to South America there are also many which concern plants occurring in New Guinea, New Caledonia, and New Zealand. These can best be explained by postulating that, while there has been much interchange of plant elements with eastern Malaysia there has also been migration from or to the north-east portions of the Australian Region through New Guinea towards New Zealand. This route appears to be distinct from that which has resulted in the occurrence of species in both Tasmania and New Zealand for which a southern route seems more probable (see Fig. 4).

There is little evidence that any important families may have originated in the Region. The possible exceptions are the Goodeniaceae and the Proteaceae. For reasons which will be discussed later, a southern origin for the latter seems quite, if not more, probable. Of the various monotypic and endemic families restricted to the Region some are probably relict in nature, such as the Cephalotaceae in the South-West Province, but others such as those in North-East Queensland may include more recently developed forms especially where separation from large, widely distributed families is not accepted by all taxonomists. However, at the subfamily and generic levels there is more ground for inferring an Australian origin, and in a number of cases, there being no clear affinity with either the route to Antarctica or that to Malaysia, it can only be suspected that the plants have developed from elements present at a very early period.

In the past, as in the present, climate has been the most important selective agent. For this reason the discussion here has been closely related to a tentative scheme of climatic variations from the early Tertiary to the present day. It seems fairly well established that the only genuinely cool period was that of the Pleistocene and for the rest the climate has varied from subtropical and wet to warm and dry. There is also some justification for stating that the seasonal nature of the climate is more marked today than, from the palaeobotanical evidence, it could have been in the early Tertiary. While the accumulation of more reliable data may contribute to a better understanding of climatic variations, it cannot be doubted that these variations provide most important clues to migrations linked with other regions and also to the changes that have taken place within the Region.

II. Palaeobotanical Considerations

(*a*) *General*

Many workers would agree with Camp (1947) in placing the origin of the angiosperms back in the Palaeozoic and it is a fact that by the Cretaceous the major groups were already well defined. Furthermore, early plant remains in New Zealand (Cockayne 1958) include records of dicotyledons linked with rocks of Lower Cretaceous age and "seed bearing" plants from the Jurassic (Oliver 1953). Camp expresses the opinion that the angiosperms first evolved on a southern land mass and later moved north to become abundant and widespread in the Eocene. He also considers that the southward movement of North American Tertiary plants was due to climatic deterioration and not primarily to population pressures resulting from the development of new forms in a northern centre of origin. One might suspect that comparable floristic changes are to be anticipated in the southern hemisphere.

Axelrod (1952) visualizes the angiosperms as having originated in upland areas under a tropical climate whence they invaded the lowlands and extended into cooler climes. He emphasizes that the centre of origin need not have been the present tropical belt since such a view is not consistent with current knowledge of fossil floras. He places this origin in Permo-Triassic times with a world distribution during the remaining Triassic and Jurassic followed by a further surge of evolution of new types in the Cretaceous. After the Cretaceous he gives the following possible development: Palaeocene–Early Oligocene, mild climate and expansion of tropical tertiary floras to latitudes 55° N. and 60° S. with consequent differentiation into various environmental types; Oligocene–Miocene, further climatic selection and segregation into latitudinal types, drier climates leading to retreat of forests and development of temperate types; Upper Miocene–Pliocene, approach to present-day conditions; and in the Pleistocene he discusses the development of vegetation types in which herbs and grasses play important roles. He also considers the presence of the Mediterranean type climate with its summer drought an important influence in promoting the development of new types and makes a special reference to the flora of south-west Australia in this connection—an opinion at variance with the palaeobotanical and cytological data available at present regarding the plants of this area. Furthermore his time scale does not accord with the evidence concerning southern hemisphere floristic affinities or the presence of what, at least today, are non-tropical "Australian" elements in the late Cretaceous and early Tertiary.

Chaney (1947) has similar views and discusses a neo-tropical Tertiary flora which ranged to approximately latitude 50° N. in the Eocene but which retreated during the Oligocene and Miocene epochs until by the Pliocene there were few remnants of it north of the Mexican border. He visualizes this neo-tropical flora as being replaced by an Arcto-Tertiary flora in the north and by an Antarcto-Tertiary flora in the southern hemisphere, the northward progress of the latter being favoured by the uplift of the Andes during the Pliocene and Pleistocene.

A somewhat similar history is postulated for Asia by Hu (1940) in a discussion on the flora of Yunnan.

In discussing the Tertiary floras of Chile and Patagonia, in relation to the present-day flora of Juan Fernandez, Skottsberg (1956) quotes from the data of Berry (1922, 1925, 1928, 1938) and of Frenguelli (1953*a*, 1953*b*) from which it would appear that there was a tropical flora in the Eocene giving way to a temperate flora in the Miocene–Pliocene. This suggests a similar succession of climates to that postulated for the northern hemisphere. Florin (1940), however, disputes Berry's opinions and considers the determinations on which they were based to be erroneous, at least so far as the conifers were concerned. He concludes that the Eocene Chilean conifers were constituents of a warm temperate or subtropical rain-forest and probably of a lowland podocarp–evergreen forest with a humid but equable climate. Florin's view is in better accord than Berry's with what the evidence suggests was the situation in Australia at the same period.

The uniformity of the climate in past ages appears to be taken for granted by many authors. Why such conditions should have existed, how they could have developed into a system of latitudinal climatic belts such as we know today, and what the intermediate conditions would have been remains obscure. It has been pointed out, however, by van Steenis (1934, 1936) that there is no reason to suppose that tropical conditions have not persisted in the Malaysian area throughout the

Tertiary and Quaternary and that the Ice Age appears to have had very limited effect on the flora. From this it may be argued that northern Australia, also, cannot have had a really cool climate during any of these periods.

(b) *Australian Region*

The early Tertiary flora of Australia was, as has already been stated, that commonly referred to as the "Cinnamomum flora" but since it included fossil species referred to *Banksia*, *Lomatia*, *Hedycarya*, *Pittosporum*, *Eucalyptus*, and *Phyllocladus*, as well as *Nothofagus* and other rain-forest types, it obviously had an Australian character that on present-day climatic tolerances is related to temperate as well as to tropical latitudes. In this connection it is interesting to find that Kryshtofovich (1929) expresses the view that the tropical nature of the Tertiary climates has been exaggerated. He uses this argument in a discussion of the history of the Tertiary flora in Asia on the basis of a North Pacific position of the North Pole with consequent warmer conditions in Europe than in Asia.

Evidence that the position of the poles has varied through geologic time is accumulating (Irving and Green 1957; Irving 1958) but its applicability to phytogeographic problems in the Australian Region is still not clear. The data suggest that Australia and the South Pole were closer together in the early Tertiary than at present and that they have been growing further apart ever since. It is difficult to correlate this with the climatic conditions indicated by the palaeobotanical record and this difficulty stands regardless of whether continental drift has or has not occurred. Irving (1958) also states that it seems unlikely that any appreciable polar wandering or relative land movements have occurred during the period since the Miocene.

Unfortunately the chronology of the Tertiary in Australia is still far from clear and though many writers consider the Cinnamomum flora to have been pre-Miocene the placements that have been given to it vary from Eocene to Pliocene (Sussmilch 1937; Singleton 1941). However, its existence during the early period is accepted by Cookson in her recent papers and by recent workers in Western Australia and South Australia.

Evidence concerning the flora which succeeded the Cinnamomum type is scanty but that available reveals an approach to the present-day flora and it is possible that the development of this new flora in southern Australia was concurrent with a displacement of the Cinnamomum type towards the north following a cooling of the climate. Whether this change represents a retreat with a consequent reduction in the area occupied or whether it was a northward migration is at present an open question but the fact remains that there are striking similarities between the Tertiary flora of southern Australia and that of certain habitats in modern New Guinea and New Caledonia. For example, Cookson (1953) in discussing *Dacrydium* shows that fossil occurrences are recorded from Denmark in Western Australia (South-West Province) through Central Australia to eastern Australia. Pollen of *Phyllocladidites*, which Cookson has identified as *Dacrydium*, has also been found in Tertiary deposits of the Kerguelen Archipelago. By contrast the modern distribution shows one species restricted to Tasmania and others in Malaysia, New Caledonia, and New Zealand as well as in South America. Another case is that of *Podocarpus* sect. *Dacrycarpus*, discussed by Cookson and Pike (1953), and having a fossil occurrence in Australia similar to that of *Dacrydium*. Cookson and Pike suggest that it may have been present in Victoria up to late Pliocene times. Today it is represented in New Guinea but not in the Australian Region. The pollen has not been found, as yet, in Cretaceous, Miocene, or Pliocene beds in New Guinea though there are living species distributed from south-east Asia to the South Pacific and New Zealand. Buchholz and Gray (1948) regard it as one of the two most primitive sections of the genus. Further evidence of the relationship between southern Australian Tertiary plants and modern representatives in New Guinea is provided by Cookson's account (1952) of the similarity of Tertiary pollen from Australia to that of living New Guinea species of *Nothofagus*.

A critical account of the data concerning fossil conifers in the southern hemisphere has been given by Florin (1940) who makes it clear that the northern and southern hemisphere members form distinct groups and, furthermore, that this separation of the family dates back to Permian or Carboniferous times. From figures indicating the past and present distribution of both *Phyllocladus* and *Podocarpus* sect. *Dacrycarpus* it is evident that they occcurred in more southerly latitudes during ancient times. Though comparable the situation in *Araucaria* is more complex. These facts support the assumption that early Tertiary floras of the Australian Region may have moved northwards following climatic changes in the Upper Miocene. So far as the Australian conifers, fossil or living, are concerned there is no evidence in favour of a northern hemisphere origin or even of an origin in the areas immediately north of the Australian Region.

In discussing the remains of fossil banksias from Yallourn in Victoria, Cookson and Duigan (1950) mention the association of these with *Nothofagus*, *Phyllocladus*, *Cinnamomum*, *Tristania*, *Casuarina*, and *Callitris*. This association of xeromorphic Proteaceae with rain-forest and "Australian" types they then compare with the conditions at present existing in the Lamington Plateau area in south–east Queensland where plant communities dominated by such xeromorphic types grow in close proximity to monsoon forest and to forest dominated by *Nothofagus moorei*. This mixture of vegetative types has also been commented on by Herbert (1950) and some of the floristic peculiarities of the area have been mentioned under the section on the MacPherson–Macleay Overlap in this paper. The climate is equable, with rainfall fairly evenly distributed over the year; it may be classed as cool tropical or subtropical and it may be compared with the climate of the mountain areas in New Guinea where *Nothofagus* forests have been found.

The occurrence of *Nothofagus* in New Guinea has been critically discussed by van Steenis (1953) and he gives some attention to distribution patterns in the southern hemisphere, especially of those plants whose occurrence points strongly to the former existence of an Antarctic land mass, and the possible significance of the occurrence of these plants in New Guinea, New Caledonia, and Malaysia. One of his points is that species occur under similar climatic conditions today and thus may be presumed to have had similar requirements in the past. *Nothofagus* occurs in New Guinea above 3000 ft altitude but not in the more humid and hotter lowlands. This fact taken in conjunction with the occurrence in the MacPherson–Macleay Overlap area plus the similarity of the Queensland assemblage with that of more southern areas in the early Tertiary and the disjunct occurrence of *Nothofagus* in cool temperate forests in high latitudes suggests that the climate at the time when the Cinnamomum flora was very widespread may have been warm temperate to tropical rather than very tropical. In this case, as van Steenis indicates, the occurrence in New Guinea is a relict formation from a northward progress.

On the other hand the Tertiary plant records are not limited to taxa of Antarctic or Australian affinities. Selling (1950) notes the presence of plants with tropical affinities such as *Elaeocarpus* (with which he equates *Penteune*, a fossil fruit of deposits in New South Wales and Tasmania), *Rhytidocaryon* (fossil Menispermaceae), *Spondylostrobus* (Burseraceae?), *Tricoilocaryon* (Sapindaceae? Burseraceae?), and *Symplocos*. He also considers that *Celyphina mccoyi* F. Muell., a fossil from Victoria, belongs under *Geoffroya*, a genus of the Leguminosae from Tropical Africa and America.

While the deposits in Western Australia have not yet been fully examined they do not suggest any great divergences from the general picture indicated by the early Tertiary deposits in south-eastern and eastern Australia. Apart from the work of Cookson and her collaborators, recent work (McWhae *et al.* 1958) on Tertiary sediments near Kojonup, in the South-West Province, has revealed the presence of *Nothofagus*, *Araucaria*, *Banksia*, and *Gleichenia* at a time which may be the same as that of the Plantagenet beds, i.e., Eocene. Thus the remarkably uniform representation of the deposits containing early Tertiary plants extends right across southern Australia and north through eastern Australia. It is generally accepted that these deposits are contemporaneous but it would be interesting to know whether a better correlation and a more definite chronological sequence might not reveal indications of south–north migration.

If the Cinnamomum flora was a type which developed in southern latitudes and was later forced to withdraw to the north under changing climatic conditions then occurrence in northern deposits (such as those in Queensland) may possibly be of a later date than some of those in the south and the lack of records from New Guinea may be due to an even later arrival in this area. If, on the other hand, the flora was of tropical origin and first spread south before it retreated north where it was limited to disjunct occurrences as is shown by modern distribution of *Dacrydium*, *Podocarpus*, and *Nothofagus*, then the northern deposits could be earlier than or contemporaneous with those of the south.

The early Tertiary flora included taxa with Antarctic affinities, such as *Nothofagus*, *Podocarpus*, and *Dacrydium*; it also included Australian elements such as *Callitris*, *Banksia*, *Casuarina*, and *Lomatia*. *Eucalyptus* may have been present, judging by fossil pollens, but its occurrence in the pre-Miocene is doubtful. Tropical elements are represented by *Elaeocarpus*, *Symplocos*, and fossil members of the Olacaceae and Sapindaceae. Thus the three main elements of the modern flora were already present even though the relative proportions were undoubtedly different. Furthermore, judging by Cookson's reports, there does not seem to have been a marked change between the upper Cretaceous and the Eocene. We have, therefore, no evidence regarding a period when one or more of these elements was missing, nor can we say whether the Australian element arose from types which migrated from the north or south or whether it represents a development from some earlier flora. There is no palaeobotanical evidence which might unequivocally support a view that the continent has not been in its present position throughout the period over which the angiosperms have shown their chief development. In particular there is nothing to suggest that the continent has drifted eastwards from a position nearer southern Africa, as has been postulated by the supporters of the Wegenerian hypothesis. Until geological or palaeomagnetic evidence definitely shows otherwise it seems best to accept the principle of continental stability at least during the Tertiary.

Apart from the palaeobotanical data a long history for many Australian elements has been indicated by their cytology. Smith White in various papers (1942, 1948*a*, 1948*b*, 1950, 1954*a*, 1954*b*) on the cytology of Australian plants has suggested a pre-Miocene origin for the Australian Boroniae (Rutaceae) and Leptospermoideae (Myrtaceae) and this, with the fossil records, supports a view that many of the genera representing the Australian element today must have arisen very early.

In recording the presence of pollen and leaf impressions of *Acacia* spp. in certain beds in Victoria, believed to be of Pliocene age, Cookson (1954) reports that *Nothofagus* appears to be absent. It is, however, present in beds of Quaternary age in the St. Kilda area, and in this case Cookson compares the pollen to that of the living species, *N. cunninghamii* (Hook.) Oerst. The more usual associates with the *Acacia* material include leaves of *Eucalyptus* (comparable with those of *E. viminalis* Labill. and *E. radiata* Sieb. ex DC.), coniferous remains and pollen of Casuarinaceae, Compositae, Haloragaceae, and Proteaceae. In the deposit with *Nothofagus* the plants present were determined as *Casuarina*, *Banksia*, *Eucalyptus*, *Haloragis*, some Gramineae, and *Cyathea australis* (R. Br.) Domin. This evidence is supported by further records of Cainozoic pollens, recorded by Cookson and Pike (1954) where the association included Casuarinaceae, Haloragaceae, Myrtaceae, Olacaceae, Proteaceae, Santalaceae, and Sapindaceae. This latter group is based on material from deposits over a wide area of southern Australia and the time range is from Eocene to Pliocene but in the case of the *Acacia* records Cookson refers most of the material to upper Miocene or late Pliocene. The leaf impressions are of the phyllodineous type and, though scarce, serve to emphasize further the Australian character of the flora which must have been present. Further evidence on Tertiary floras is given by Patton (1958). It seems possible that at least two plant communities may have been present even during the Cinnamomum period. The greater prevalence of the "Australian" types in Pliocene deposits suggests, since it indicates a reduction in the area carrying *Nothofagus*, that the rain-forest type was already moving or retreating northwards and hence this movement was not primarily due to the onset of the cooler conditions of the Pleistocene as is suggested by Baur (1957). This change also indicates that there has been a shift from the humid conditions and equable climate, which apparently suited *Nothofagus*, to a more seasonal climate favourable to the development of the "Australian" elements.

Evidence concerning past climates in the southern hemisphere is limited, though work by soil scientists and others is beginning to clarify the picture so far as Australia is concerned. The information at present available is still under consideration and analysis and hence the remarks made here must be regarded as highly tentative and subject to correction when the results of current research are published. The author is particularly indebted to Mr. R. W. Jessup, Division of Plant Industry, C.S.I.R.O., for advice in this matter but it should be understood that he cannot be held responsible for any errors in the opinions expressed or the assumptions made here.

Work in South Africa, particularly that concerned with the dating of archaeological remains, by Smuts (1938) and by Cooke and Clark (1939) has contributed knowledge of climatic sequences in that continent. From this it is clear that there was an alternation of wet and arid cycles comparable to that known to have occurred in Australia. A similar alternation of dry and wet phases has been reported from the post-Pleistocene in southern Chile. Salmi (1955), in a study of cave deposits at Ultima Esperanza containing remains of the ancient giant sloth, reports that the animals fed on the plants of a steppe type vegetation. This vegetation is believed to have been developed under warm and arid climatic conditions, coinciding with a retreat of the local glaciers, which occurred between forest periods when the glaciers were more extensive. The period in question is, on the basis of a radiocarbon dating, given as 10,832±400 years ago. This would lie in the postglacial stage according to Tindale's (1947) correlation of Pleistocene times in South Australia with those in the northern hemisphere.

As a tentative scheme the climatic sequence in Australia appears to have been as follows. Subtropical climates may have persisted throughout the Eocene and most of the Miocene but there may have been a change to semi-arid conditions in the upper Miocene. Possibly the reduction of the *Nothofagus* areas in Victoria and the correlated increase in the incidence of *Acacia* reflects this change. Later, in the Pliocene, there was a swing back to subtropical conditions but since there was not a corresponding increase in *Nothofagus* it may be suspected that the climate had more strongly marked seasonal variation than seems to have been the case in the early Tertiary. The Pleistocene was at first arid but conditions became very wet in the later stages during part of which temperatures were mild or warm though they became cool during the period of glaciation (Browne 1945). Ice sheets were very limited in extent (Browne 1957; Jennings and Banks 1958) and only existed in areas of Tasmania and on the highest levels of the Australian Alps. Arid conditions returned at the end of the Pleistocene or the beginning of recent times. It is interesting to make a comparison between these wet and dry phases in Australia and the Kalahari wet and dry phases in South Africa (Cooke and Clark 1939). These authors tabulate three subsequent wet and dry periods for their area and there is some evidence that there have been similar climatic oscillations in Australia but the number and relative intensity of these is not yet fully understood. It may be said, however, that the present climate represents an arid phase.

It is difficult to make satisfactory comparisons between climatological data relevant to the land floras and the palaeontological data concerning marine fauna. Nevertheless it is interesting to find that Crespin (1948) in discussing the "Indo-Pacific influence" in the foraminiferal assemblages, present in Tertiary beds from the North-West Basin in Western Australia around the south coast to north-west Victoria, writes: "The conclusion drawn from the above observations is that Indo-Pacific conditions extended down the coast of Western Australia, across the southern part of the State into South Australia and north-western Victoria in Middle Miocene to early Upper Miocene ("f_2–f_3") time, with a very limited extension into southern Victoria. Then followed a gradual recession of conditions. No Pliocene deposits containing Indo-Pacific forms are known east of the Adelaide Plains and the sections south of Adelaide along Gulf St. Vincent. According to Cotton, of the South Australian Museum, the examination of molluscan faunas in South Australia suggests that this recession has continued westwards during Pleistocene and Recent times."

It is inferred that the recession mentioned indicates a cooling of the local waters and if so there may be a possible relationship with the floristic changes on the land surface at about the same time. What the significance of the westward "recession" might be for the phytogeographer is not clear, since it must be related as much to ocean currents as to land climates; but it could mean that milder or warmer conditions persisted in the west longer than in the south and south-east.

Crespin's results have been somewhat modified by more recent studies by Ludbrook (1954) on the Pliocene Mollusca from beds underlying the Adelaide Plains. This work is still in progress. She recognizes four elements: Indo-Pacific, Tethyan Eocene, Australasian, and Cosmopolitan. In her view there was no sudden temperature or ecological change which could have resulted in extinction of the marine fauna between the Eocene and Middle Pliocene. During these periods thermal conditions appear to have been very uniform—a state of affairs in accordance with the scanty palaeobotanical data concerning land floras apart from the possible semi-arid phase of the late Miocene.

Lacking accurate information concerning world air circulation in the geologic past we can only view such such climatic changes in the light of present-day conditions. According to Willett (1953) the world air circulation may be assumed to have had the same primary pattern from the Pleistocene to the present day since there have been no major changes in the topography of the continents and oceans. Because of this, it is possible to review climatic oscillations by considering the effects of possible variations in the current pattern.

The climate of the Australian Region is controlled to a large degree by the route followed by the Antarctic low-pressure systems which bring winter rain storms in the south and by the intensity of the summer storms in the north and north-east. Various authors, including Gentilli (1949) have discussed the effect of a change in the position of the route traversed by the Antarctic lows. A reduction of the South Polar Ice Cap shifts this route southwards and the effect is a lessening of the influence of the storms in southern Australia. Similarly an increase in the area of the Ice Cap would result in a greater area of southern Australia being affected by winter storms. It seems reasonable to infer that the latter condition existed during the Pleistocene pluvial phases. Gentilli suggests that while the south was "pluvial" the northern areas would have been much drier owing to a northward transposition of the dry tropic belt. This has been accepted in principle by Specht (1958) but it rests on the assumption that this dry belt of the middle latitudes would be so transposed with a resultant narrowing of the equatorial wet tropics and also that the two hemispheres are climatologically out of phase.

According to Willett (1953) the evidence now available indicates that the major glacial–interglacial cycles of the two hemispheres may have been in phase and not in opposition. Under a "glacial" climate the intensity of the storms, and hence of the precipitation, is increased in all zones. Increases in the area of the polar ice caps result in intensified air circulation in latitudes lower than those currently affected by storm paths, pluvial conditions extend to middle latitudes, and the equatorial easterlies are strengthened. By contrast, in interglacial phases the rate of air circulation falls, storm intensity is reduced, and annual rainfall decreases in all zones. Storm systems in polar regions retreat into higher latitudes, tropical systems are weaker, and there is a broadening of the arid belt in the dry tropics. If this was so then the arid area in Australia would contract in a glacial phase and expand in an interglacial.

Nevertheless many authors do not consider that the climates of the two hemispheres are in phase to this extent. Lamb (1959), for example, shows that at least the minor oscillations are out of phase. He gives an instance when an apparent rise in temperature in southern latitudes can be correlated with a colder period in the Arctic Polar regions. This author discusses the importance of the southern westerlies and states that they influence climate over a large area of the globe. At present these westerlies are strong enough to be related to the fact that the meteorological equator lies slightly to the north of the geographical one. Unfortunately the nature of the relationship between equatorial climate and changes in thermal conditions over the poles is still not properly understood. From Lamb's remarks it would seem that, under out-of-phase conditions, there could have been some latitudinal shifting of the major wind systems in one or other of the hemispheres but this does not necessarily mean a retention of a wide dry tropical belt during pluvial phases with correlated increased rates of air circulation.

From the information provided by Watts (1955) regarding Equatorial Air Stream boundaries it would seem that ratios between the rates of circulation in the two hemispheres would have a profound effect. Thus if the rate was higher in the southern hemisphere there could be, for example, an increase in the effect of the South Indian Ocean air stream on the precipitation from the South-West Monsoon. This monsoon is, however, dependent upon the intensity of the high pressure system developed over Tibet and Siberia.

Flohn (1958) states that during the summer the main westerly air stream passes to the north of the Central Asian elevated block and winds to the south are easterlies. In the winter these latter are replaced by strong westerlies. Ramage

(1952) has described the convergence of these with the south-westerlies in the Bay of Bengal and the relationship of the combined air stream with the generation of storm centres in the Pacific. If the climates of the hemispheres were in phase, then under a glacial cycle the westerlies would persist for longer periods and an increase in the number of storms related to this system could be anticipated. The path followed would not necessarily be transposed because of the correlated increase in rate of circulation in the southern hemisphere. If the climates were out of phase then the result could be, so far as Malaysia is concerned, a change from an equably wet climate to one in which precipitation was more seasonal in its incidence, though higher than in the dry tropics.

From the modern distribution of plants in the islands of the Near North it seems probable that if this condition existed then the climate cannot have been completely seasonal but if it occurred when communication was possible with the Australian mainland then it provides a set of conditions under which Australian elements could have migrated into Malaysia.

One does not wish to carry speculation on meteorological features too far but it is worth recording certain evidence that supports the view that higher rainfall occurred in both northern and southern Australia during pluvial cycles. Thus pedological data indicate that laterites, whose formation requires a warm wet climate, developed over wide areas of Australia during more than one stage of the post-Pleistocene but there is no evidence that this process occurred at different times in the north and the south. Again, in northern Australia certain species with strong Malaysian affinities occur in disjunct areas (Specht 1958). Arrival of many of these should probably be related to the Pleistocene land continuity with New Guinea but it is difficult to understand their migration if the north was arid. An earlier arrival would, in most if not all cases, be unlikely and a later one impossible owing to a lack of a possible route. Further, and as a final example to support the view that there has been expansion and contraction of the arid areas, one may state that the distribution of endemic genera within the Eremaea does not indicate that there has been any marked transposition of the arid centre. This point will be further discussed in a later section.

III. The Australian Floristic Elements

It is customary to divide the Australian flora into three elements, the Australian or autochthonous element, the Antarctic element, and the Tropical element (variously referred to as "Malayan", "Malaysian", or "Indo-Melanesian"). It will be obvious that such terms have their special meaning only within the Australian Region since the point of view from which migrations and affinities are considered will be quite different in other phytogeographic regions. For example, the term "Australasian" is commonly used to cover the Australian and New Zealand areas, despite the great and basic differences in their respective floras, but certain European writers employ it for the Asia–Australian region and van Steenis (1953) has used it for a group of plants distributed in Australia, Tasmania, New Zealand, and eastern Malaysia. Similar difficulties arise over the use of the term "Malaysian" which in this paper is used to cover the area dealt with by contributors to the *Flora Malesiana* now in course of publication, under the editorship of van Steenis, despite some ambiguities concerning its boundaries.

The Australian flora includes two lesser floristic elements which are often overlooked. One of these includes the cosmopolitan genera for which, in the absence of data concerning centres of origin, it is particularly difficult to suggest migration routes. The other includes taxa which appear to have affinities with plants in the northern hemisphere. This group can be subdivided into temperate elements, such as *Euphrasia*, *Viola*, *Ranunculus*, etc., whose affinities with species in high southern latitudes requires investigation, and arid or semi-arid elements found amongst the Eremaean flora. Further reference will be made to these groups in a later section.

TABLE 16

FLORAL ELEMENTS IN THE AUSTRALIAN FLORA, BASED ON THE FLORA OF ARNHEMS LAND

After Schwarz (1928)

	Element	Facies
Austral Floral Complex	Australian	Tropical South-East Australian South-West Australian Central Australian
	Melanesian	York Tasmanian
Asiatic–African Floral Complex	Indo-Malaysian	Carpentaria East Malaysian

As might be expected on grounds of climatic tolerances as well as on historical ones the representation of the floristic elements varies within the main zones. This has already been discussed in the first part of this paper where it was suggested that the "tropical" elements found in the Temperate Zone may be the descendants of early migrants, that many of the smaller genera in the Tropical Zone are so closely related to plants in the Malaysian area that a recent arrival in the Australian Region seems probable, and finally that there are elements in the Eremaean flora which are unlikely to have arisen in the Region but which are also unlikely to have reached the Zone by migration through either the Temperate Zone or the Tropical Zone by any path which would have involved competition with the chief communities of these zones.

Schwarz (1928) has discussed the phytogeography of the flora of northern Australia with special reference to the plants of Arnhem Land. While much of his data must be regarded as superseded by those available to Specht (1958) it is interesting to see how he distinguishes between the elements represented in the flora. This is shown in Table 16.

There is a certain similarity between Schwarz's scheme and the views adopted here but it will be noted that he makes no reference to Antarctic elements now represented or isolated in tropical regions. His Tropical Facies corresponds with the Tropical Zone except for the omission of the Pilbara District in Western Australia and the inclusion of portion of southern New Guinea and southern Celebes. It is possible that he is correct in the latter case but consideration of the flora of New Guinea has been omitted from this discussion because of lack of adequate data and because the area is being critically studied by other workers at the present time. Schwarz's South-East and South-West Facies form the Temperate Zone of this paper; his Central Australian Facies may be equated with the Eremaea though his boundaries are not exactly similar. His Melanesian element may be compared with the comments made in this paper concerning genera occurring also in New Guinea, New Caledonia, and New Zealand (see Table 7 under South-West Province) and also the affinities between Tasmania and New Zealand (see under Tasmania).

While affinities can be traced when distributions extend to other regions the recognition of "Australian" elements is not a simple process. We have to make considerable use of the argument of probability as a basis for saying that certain taxa, whether they be families, genera, or species, have arisen within the Australian Region. While this is justifiable for the purposes of a discussion of this nature it should be kept in mind that the criteria should include adequate data of palaeobotanical, distributional, and also cytotaxonomical relationships. Information of the first and last of these being inadequate or almost completely lacking, statements regarding centres of origin can only be tentative. "Australian" elements in this sense may include firstly those which originated in Australia in some very early period independent of the migrations from either Antarctica or Malaysia, believed to have occurred since the pre-Cretaceous, secondly those which have evolved from types which entered over the periods of these later migrations, and thirdly types which have developed as a result of the selective effects of climate and habitat and which may have as ancestors plants from either of the first or second groups or from both. Consequently, while it is customary to use the term "Australian element" with particular reference to the sclerophyllous plants so characteristic of the Temperate Zone (though present in all three main zones), there is no reason to suppose that these are the only elements which should be regarded as truly "Australian". Undoubtedly there are types limited to either the Tropical Zone or the Eremaea which, though not sclerophyllous, are as genuinely endemic elements in a floristic and phytogeographic sense. The fact that the history of some may be traced back to the Cretaceous while others are of more recent origin or are of unknown history is irrelevant.

Diels (1906) and Wood (1930) consider that there may have been an extensive Australian flora prior to the disruption of the continent by Cretaceous marine invasions. Crocker and Wood (1947) express the opinion that the breaking up of the continent at this period may not have been as extensive as is sometimes thought but in all these cases the authors are considering the relationships between the "Australian" elements in south-west and in south-east Australia. In the present author's opinion it is not necessary to rely on such an early isolation of west and east to account for the main differences between these areas (see under South-West Province) since it would have been prior to the development of the very extensive, uniform, and distinctive flora of the Eocene. Nevertheless, since some of the characteristic Australian genera were present in this epoch the early isolation must be of some importance. The degree of this importance cannot be gauged until more information is available concerning the flora which must have preceded the Cinnamomum one. As yet we know very little of any angiosperms which may have been present, though Glaessner and Rao (1955) report cycads and conifers from the Lower Cretaceous.

In discussing the occurrence of *Nothofagus* in New Guinea van Steenis (1953) recognizes four types of distribution, in the Pacific, of plants which may have had an Antarctic origin. One type includes plants limited to a circum-South Polar distribution, a second group (which he calls "Australasian") occurs in Australia, Tasmania, New Zealand, and Malaysia; the third group is similar to the first but includes New Guinea endemics and plants extending to islands of the Pacific, including Hawaii, while the fourth group is similar to the first and second but its representatives occur outside the Pacific area. Skottsberg (1953), on the other hand, distinguishes between "Austral" and "Sub-Antarctic" groups and relates these not only to their climatic tolerances today but to different plant associations—montane and lowland—on the Antarctic continent in earlier times. Both authors refer to plants in Australia (or in Australia and the adjacent areas to the north) but it is not easy to apply their groupings to the Australian floristic data. The fossil floras of southern Australia seem to have included, as has already been mentioned, elements of both "tropical" and "Antarctic" types but among the latter are genera such as *Podocarpus*, *Dacrydium*, and *Nothofagus* whose species in Malaysia and the warmer areas of the Pacific have special affinities with fossil taxa from southern Australia. Consequently it is difficult to distinguish between Antarctic elements which may now have become wholly centred in the tropics and tropical elements which, having extended south in the Tertiary, are now mainly tropical in distribution though in some cases represented by southern relicts. More data might enable us to separate these into "palaeotropical" and "palaeoantarctic" types but for the present we can only assume that both occur. Unfortunately the first of these terms has come to apply to the plants of the "Old World tropics" rather than to plants of tropical areas in ancient times as would seem natural when the term is employed in a discussion of palaeobotanical matters. So far as the Australian Region is concerned it is probable that the term can be applied in both senses but in order to clarify the matter it may be desirable to employ the new term "priscotropical" (based on *priscus*, meaning "belonging to former times").

That palaeoantarctic elements are present in the tropics is indicated by past and present distribution patterns but it seems likely that in some cases the origin was northern and not southern and consequently each case requires careful analysis. For example, Lam (1940) has suggested that the Sapotaceae, which are now wholly tropical, may have had an Antarctic origin. If this was so then the Australian representatives could be of either northern or southern origin. However, since they do not seem to represent the most primitive types and since they are limited to the Tropical Zone and to the MacPherson–Macleay Overlap a northern origin appears the more likely so far as these particular modern species are concerned.

If the Proteaceae are regarded as being of Antarctic origin then some of their northern representatives may possibly be palaeoantarctic in nature since the fossil records for the northern hemisphere are not beyond question (Cookson and Duigan 1950). Of the two subfamilies, the Persoonioideae include 14 modern genera limited to South Africa and 12 restricted to the Australian Region, apart from the single non-Australian species of *Persoonia*. Of the 12, three are monotypic and restricted to Tasmania, three are restricted to the South-West Province of Western Australia, one is endemic to parts of New South Wales, *Persoonia* has groups of species in the South-West Province and in south-eastern and eastern Australia and the others, *Adenanthos*, *Conospermum*, *Isopogon*, and *Petrophila* all have their major development in the South-West Province but are also represented in other parts of the Temperate Zone. Except for *Persoonia falcata*, which is closely related to the species of the South-West Province, none is found in the Tropical Zone and none occurs in the Eremaea. On the other hand the distribution of the Grevilleoideae is quite different (see Figs. 5 and 6), there being 23 genera distributed as follows:

(1) Fourteen genera are endemic to the Australian Region and fully restricted to it. Two others have a few species outside the Region (*Banksia* and *Grevillea*).

(2) *Dryandra* is restricted to the South-West Province and fossil evidence of wider distribution in the past is not reliable.

(3) Seven genera (six monotypic) are restricted to North-East Queensland. These are *Buckinghamia*, *Cardwellia*, *Darlingia*, *Hollandaea*, *Musgravea*, *Opisthiolepis*, and *Placospermum*.

(4) *Hicksbeachia* is restricted to the area from North-East Queensland to the MacPherson–Macleay Overlap.

(5) Three genera have markedly discontinuous distributions. These are *Lambertia* (nine species in South-West Province, one species Hawkesbury Sandstone areas of New South Wales); *Strangea* (two species in South-West Province, one species in south-east Queensland); *Xylomelum* (two species in South-West Province, two species in North-East Queensland to coastal New South Wales) and finally *Telopea* which is eastern and found from the Dividing Range in New South Wales through Victoria to Tasmania but in disjunct areas.

(6) No genus is restricted to Tasmania and none has an area of major development in south-eastern Australia.

(7) Nine genera are not restricted to Australia. *Banksia* (40 spp.) has one species in Malaysia, *Gevuina* occurs from Malaysia to South America and has one endemic species in North-East Queensland; *Grevillea* (250 spp.) has two species extending to New Guinea, the Moluccas, and Celebes, there is also one endemic species in New Guinea and one in Celebes. *Helicia* has its major development in Malaysia but there are seven or eight species between North-East Queensland and the MacPherson–Macleay Overlap;

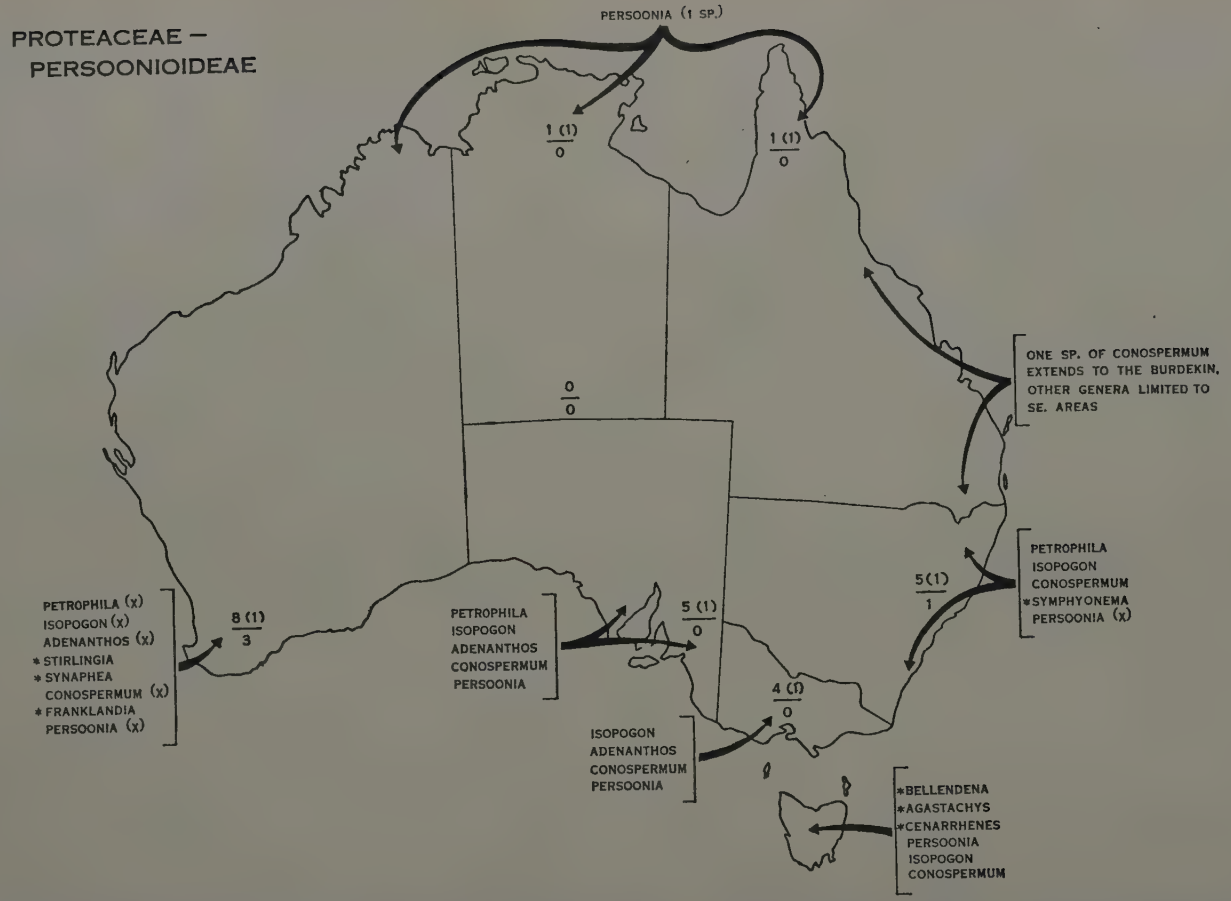

PROTEACEAE – PERSOONIOIDEAE
PERSOONIA (1 SP.)
1 (1) / 0
1 (1) / 0
0 / 0
ONE SP. OF CONOSPERMUM EXTENDS TO THE BURDEKIN. OTHER GENERA LIMITED TO SE. AREAS
PETROPHILA
ISOPOGON
CONOSPERMUM
*SYMPHYONEMA
PERSOONIA (x)
5 (1) / 1
PETROPHILA (x)
ISOPOGON (x)
ADENANTHOS (x)
*STIRLINGIA
*SYNAPHEA
CONOSPERMUM (x)
*FRANKLANDIA
PERSOONIA (x)
8 (1) / 3
PETROPHILA
ISOPOGON
ADENANTHOS
CONOSPERMUM
PERSOONIA
5 (1) / 0
4 (1) / 0
ISOPOGON
ADENANTHOS
CONOSPERMUM
PERSOONIA
*BELLENDENA
*AGASTACHYS
*CENARRHENES
PERSOONIA
ISOPOGON
CONOSPERMUM

Fig. 5.—Distribution of the Proteaceae–Persoonioideae in the Australian Region. An asterisk marks each genus restricted to a particular area and (x) indicates a large number of species in an area. In each ratio the upper number gives the number of genera and, in brackets, those occurring outside the Region. The lower number refers to restricted endemics.

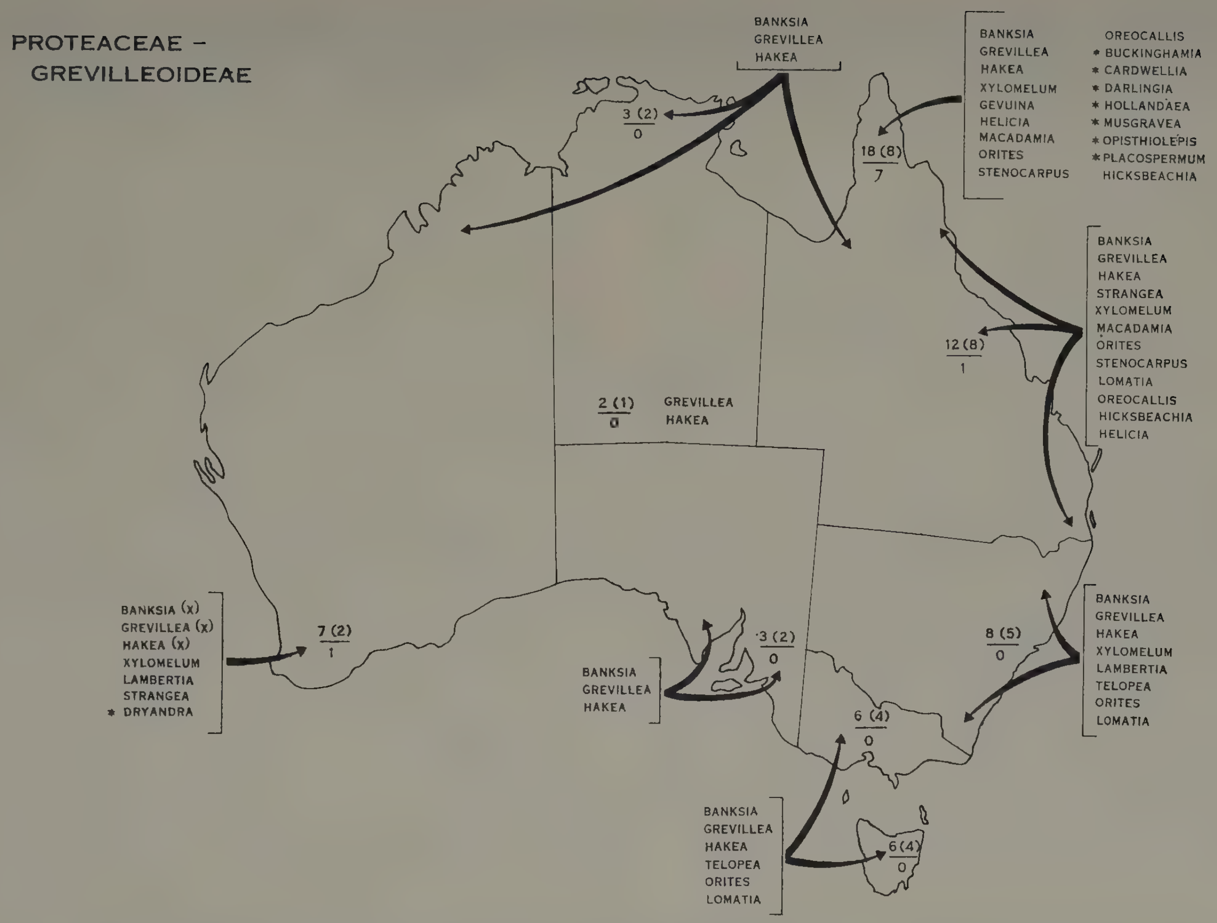

PROTEACEAE –
GREVILLEOIDEAE
BANKSIA
GREVILLEA
HAKEA
3 (2) / 0
BANKSIA
GREVILLEA
HAKEA
XYLOMELUM
GEVUINA
HELICIA
MACADAMIA
ORITES
STENOCARPUS
OREOCALLIS
* BUCKINGHAMIA
* CARDWELLIA
* DARLINGIA
* HOLLANDAEA
* MUSGRAVEA
* OPISTHIOLEPIS
* PLACOSPERMUM
HICKSBEACHIA
18 (8) / 7
BANKSIA
GREVILLEA
HAKEA
STRANGEA
XYLOMELUM
MACADAMIA
ORITES
STENOCARPUS
LOMATIA
OREOCALLIS
HICKSBEACHIA
HELICIA
12 (8) / 1
2 (1) / 0
GREVILLEA
HAKEA
BANKSIA (x)
GREVILLEA (x)
HAKEA (x)
XYLOMELUM
LAMBERTIA
STRANGEA
* DRYANDRA
7 (2) / 1
BANKSIA
GREVILLEA
HAKEA
3 (2) / 0
8 (5) / 0
BANKSIA
GREVILLEA
HAKEA
XYLOMELUM
LAMBERTIA
TELOPEA
ORITES
LOMATIA
6 (4) / 0
BANKSIA
GREVILLEA
HAKEA
TELOPEA
ORITES
LOMATIA
6 (4) / 0

Fig. 6.—Distribution of the Proteaceae–Grevilleoideae in the Australian Region. Symbols as in Figure 5.

Lomatia is also in South America but there are eight species in the area from south-east Queensland and Tasmania; *Macadamia* extends from Celebes to New Caledonia with five species between North-East Queensland and the MacPherson–Macleay Overlap; *Orites* occurs in South America but there is one species in North-East Queensland and seven species between south-east Queensland and Tasmania (generally at higher elevations); *Oreocallis* has two endemic species in the area from North-East Queensland to the MacPherson–Macleay Overlap and is also represented in New Guinea and South America; *Stenocarpus* has four species of which two are endemic and occur in North-East Queensland and the MacPherson–Macleay Overlap while two extend to New Guinea and New Caledonia (see Fig. 7).

(8) The three largest genera—*Banksia* (40 spp.), *Grevillea* (250 spp.), and *Hakea* (140 spp.)—each have a centre of development in the South-West Province but only *Dryandra* is wholly restricted thereto.

It is thus evident that while both subfamilies are in Australia, and are generally regarded as Australian elements, they have different distribution patterns. The Persoonioideae are mainly in South Africa, the South-West Province, and south-eastern Australia with a special group of endemics in Tasmania. The Grevilleoideae, on the other hand, are closely related to South American taxa, despite the absence of endemics in Tasmania (the nearest portion of the Australian Region) and there is a distinct group of tropical representatives in North-East Queensland (see Fig. 6).

In a recent cytotaxonomic study Rao (1957) suggests that the Persoonioideae are the more primitive group. He also suggests that since both subfamilies are present the family may have originated in the Australian Region. However, the problems relating to migration from the Region to both South Africa and South America raise difficulties in time as well as geographically (since there is little evidence of their having migrated *south* during the Tertiary) and it still seems necessary to include the possibility that there was a development of the original forms in an Antarctic land area from which both the main types reached Australia but only representatives of one of each migrated to South Africa and South America. If it could be demonstrated at the generic level that the Persoonioideae had a centre of origin in Western Australia and the Grevilleoideae in eastern Australia then it could be postulated that the family originated in the Australian Region and that migration of the one to South Africa and the other to South America took place during some period when the continental masses were in closer proximity to one another than they are at the present time, i.e., there would be evidence in favour of the modified Wegenerian hypothesis. Cookson and Duigan (1950) record both subfamilies present in the early Tertiary but the data do not allow a geographic analysis and an Antarctic centre of origin is further indicated by the presence of Proteaceae in Eocene deposits from Chile (Skottsberg 1956).

The distribution of the members of the Grevilleoideae which reach Malaysia has been discussed by Sleumer (1955) in his account of the family for the *Flora Malesiana* where a distribution map shows the relationships of some with those in Australia and South America (Fig. 7). Sleumer also refers to the fact that many species are particularly resistant to fires. As has been shown by Gardner (1957) and by Specht, Rayson, and Jackman (1958) there are Australian plant communities which include a number of species apparently well adapted to periodic fires. Furthermore the fauna associated with such plant communities may also be so adapted (Bornemissza 1954). Among the plant species are a number of Proteaceae such as *Hakea multilineata* Meissn., *H. platysperma* Hook., *H. crassifolia* Meissn., *Xylomelum angustifolium* Kipp., as well as species of *Banksia* and *Persoonia*. In many cases the seed vessels do not open except after a fire or a long period of drying or even death of the parent plant. Some of the species are constituents of heath associations but others are found in eucalypt forests where a lower storey of *Banksia* or *Xylomelum* has a density and vigour related to the period since the area has been burnt. The longer this period the thinner the representation. From this it may be argued that the Proteaceae, especially the Grevilleoideae, have long been adapted to a climate in which annual droughts are customary, for only under conditions with seasonal variation with a marked dry period is resistance to the effects of fire likely to be advantageous. In this connection it is interesting to find that a number of the Proteaceae in Malaysia occur in areas with a seasonal monsoon climate. The association of "Australian" elements in Malaysia with this type of climate has been commented on by Airy Shaw (1942).

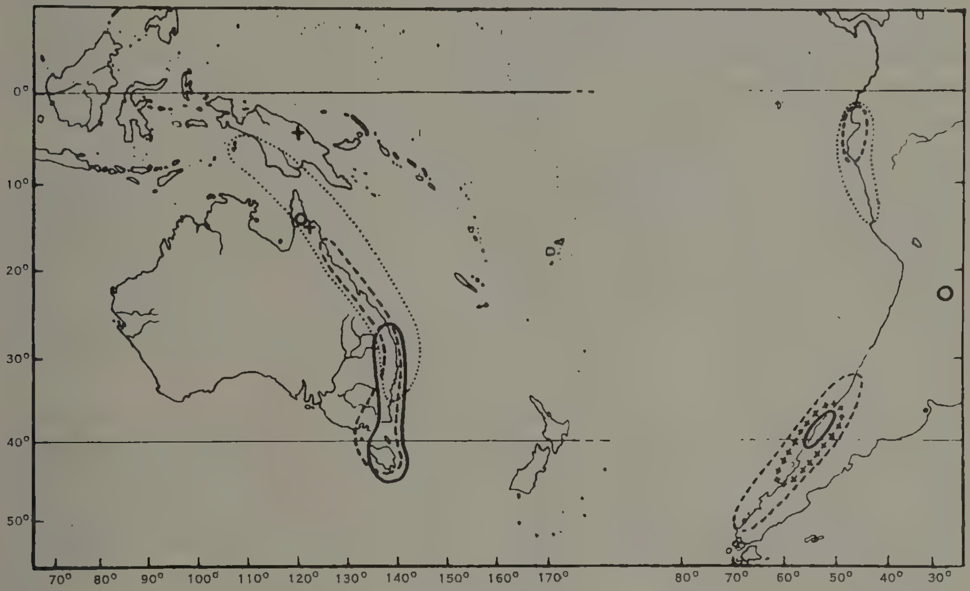


Fig. 7.—Distributional areas of the bicontinental proteaceous *Orites* (————), *Gevuina* (++++), *Lomatia* (– – – –), and *Oreocallis* (. . . .). For convenience part of the Central Pacific is contracted. (After Sleumer (1956).)

It was pointed out by Specht and Rayson (1957) that the heath vegetation in South Australia contains plants that have a growth phase out of rhythm with the present Mediterranean-type climate. These plants make their major growth during the drier months of summer when it would have been anticipated that their leaves would be close to wilting point. This feature is consistent with observations made by the present author when in Western Australia where a large number of species of *Eucalyptus* have two distinct periods of growth and stem elongation—one in spring and a more pronounced one in late summer when soil moisture levels are low. A number of species of *Banksia* and other Proteaceae produce their maximum growth during the driest months of summer, this activity following the production of flowers. Other plants which produce their major vegetative growth during the summer drought include species of *Scaevola* and *Dampiera* (Goodeniaceae). The significance of the growth rhythms in these plants is not fully understood but it is thus evident that a number of southern Australian genera, which can on general grounds be considered as members of the autochthonous element, reveal a certain lack of complete correlation with the Mediterranean-type climate in which so many of them now live. The most likely explanation seems to be that they retain some of the growth rhythms belonging to the climatic regimes of earlier periods. Specht (1958) favours the view that these plants have developed from forms which originated in tropical areas, but the fossil records reveal their long history in southern Australia, and the fact that they are less numerous not only in the Eremaea but also in the northern tropical areas of the Region suggests that their distribution in southern and eastern Australia at the present time is due to something more fundamental than a partial adaptation to a temperate climate.

Though proteaceous remains have been recorded from deposits in the northern hemisphere many of the reports appear to have been based on erroneous determinations, though the matter is still in doubt. However, the close relationship of the family with climates of a seasonal type in the southern hemisphere, plus the fact that the present Malaysian representatives do not appear to represent a centre of origin, means that the postulation of a southern origin is in closest accordance with the problems arising from the distributional patterns.

The author does not consider that the major proportion of the autochthonous elements originated in tropical areas or developed from elements which migrated from the tropics to the north of the Region, but there are undoubtedly taxa with tropical affinities present in non-tropical areas of the Region and it is possible that some of these may be identified by a study of their growth rhythms. Thus the Sapindaceae are mainly tropical and those within the Australian Region cannot logically be regarded as of Antarctic origin or as representing an Australian centre of origin for the family. Consequently it is significant that *Heterodendrum*, though endemic to the Region and very widespread in the Eremaea, has a strikingly high optimum temperature for germination. In a test by the author the range was 85–95°F (30–35°C) and higher temperatures up to 104°F (40°C) were tolerated. It may be due to this as well as to the low level of seed-set that, at least in the southern portions of the distributional range, this species reproduces mainly by vegetative means. These temperature tolerances in *Heterodendrum* are considerably higher than those required for germination in other common Eremaean species such as *Acacia aneura* F. Muell., *Atriplex vesicaria* Hew., and *Kochia sedifolia* F. Muell.

Another family which probably originally entered the Region along a northern migration route is the Myrtaceae but in the two subfamilies Chamelaucoideae and Leptospermoideae there has been a great deal of evolution within the Region. As pointed out by Smith White (1942, 1948*b*, 1950, 1954*b*), the Chamelaucoideae are wholly Australian and the chief centre is in the South-West Province. The Leptospermoideae are centred in the Australian Region but a few species occur in Malaysia and north to the Philippines while the subtribe Metrosiderae has a centre of development in south-east Asia and extends to New Zealand and America. This subtribe is not represented in the South-West Province. The few representatives of the Myrtoideae which reach Australia are restricted to the warmer high-rainfall areas, particularly those in north-eastern Australia. None has been reported in Tertiary deposits (Duigan 1951) and none is known from either the South-West Province or Tasmania.

Smith White considers that the Leptospermoideae and Chamelaucoideae had different origins from the original Myrtiflorae stock to that of the Myrtoideae. In his most recent paper (1954*b*) he accepts the tribe Chamelaucinae (Euchamaelaucinae) as being specialized and derived from forms with a basic chromosome number of $n = 11$. This would suggest that the Leptospermoideae are the more primitive group. Among Tertiary deposits the Leptospermoideae seem to be the only ones reported but the significance of this remains to be seen as the majority of the fossils are placed with *Eucalyptus*, *Tristania*, and *Callistemon*, i.e. with genera including species now associated with higher rainfall conditions. It is therefore possible that the absence of the Chamelaucoideae is due to their association with dry habitats, where there was an absence of conditions suitable for preservation. Smith White suggests (loc. cit.) an origin in the Eocene or Miocene for the Chamelaucinae but this is not yet borne out by palaeobotanical records. However, the wide distribution of *Darwinia*, *Homoranthus*, and *Verticordia* indicates an existence long prior to the great break in the floristic regions of west and east, a break whose most important phase seems to have been in the late Pleistocene.

On the whole the evidence seems to favour a northern origin and point of entry, presumably during the Cretaceous or even earlier. At least some of the more important genera were already developed by the Eocene but it is possible that there was a great development in southern Australia during the Pliocene and Pleistocene with adaptation to the more seasonal type of climate and drier conditions. Doubtless some of the earlier types survived by migrating north with the *Nothofagus* forests though, so far as *Eucalyptus* is concerned, the occurrence of Corymbosae types such as *E. clavigera* and *E. papuana* (both sensu Blakely) in New Guinea may be due to later migration or to survival from the early Tertiary continuity with Australia.

In *Eucalyptus* changes in climate have probably had an important influence on the sorting out of the subgeneric categories into different climatic areas. The Corymbosae, for example, seem to be an early type that requires warm conditions preferably with at least some summer rain. The main concentration of these is now in the Tropical Zone but a few species are found in the South-West Province and there are a few in the coastal areas of eastern Australia. A warm climate origin for this type is also indicated by their habit of producing new growth during the later summer months, in southern regions, whether there is or is not a local seasonal drought. Species of the Corymbosae may have existed in Tasmania during the Tertiary but we have no evidence to show whether they persisted until the glaciation and cold climate of the Pleistocene. In contrast to the Corymbosae are those species in which the leaf venation becomes almost longitudinally parallel. Such species as *E. pauciflora* Sieb. and *E. stellulata* Sieb., which exhibit this type of venation, are associated with cool or cold climates and with the mountain areas of south-eastern Australia and Tasmania. The earliest fossil record of this type is that of *E. precoriacea* Deane from the Sentinel Rock beds (coast of Victoria to north-west of Cape Otway) which also contain plurinervate phyllodes of *Acacia* (Cookson 1954), but the possibility remains, as was recognized by Deane, that the leaves belong to *Acacia* and not to *Eucalyptus*. Cookson reports that according to Singleton the deposits are underlain by beds of Lower Miocene age and overlain by others of Pleistocene age. If the fossils do truly represent *Eucalyptus* leaves of the parallel-nerve type it is curious that this type has not become more widespread and also that it should have occurred under much warmer conditions than those tolerated today. Another derived form is that of the Mallee type for which parts of Western Australia, particularly Interzone 1, may be the primary centre (Burbidge 1952). This type is southern and associated with the drier temperate areas. It is particularly well adapted to periodic burning (Gardner 1957) and has probably developed since the Tertiary and possibly since the Pleistocene.

It thus appears that *Eucalyptus* may have originally evolved under conditions of warm climate and warm season precipitation since certain primitive types are found in northern Australia and Western Australia. The major development seems to have been in southern areas where forms adapted to a seasonal climate with winter rainfall are numerous, but forms adapted to dry temperate or arid conditions or to cold temperate conditions have also been evolved. That there may be a relationship between the evolution of the subgeneric taxa in *Eucalyptus* and the development of an increasingly seasonal type of climate was noted by Andrews (1913, 1916). This author considered that *Eucalyptus* may have evolved from one of the Metrosiderae during the Cretaceous and in the northern areas of Australia. Southward expansion resulted in the development of the various sections in response to the colder climate and the poorer soils. The genus is seen as developing from a Corymbosae type, which largely remained in the north but whose area was subsequently invaded by the later southern forms.

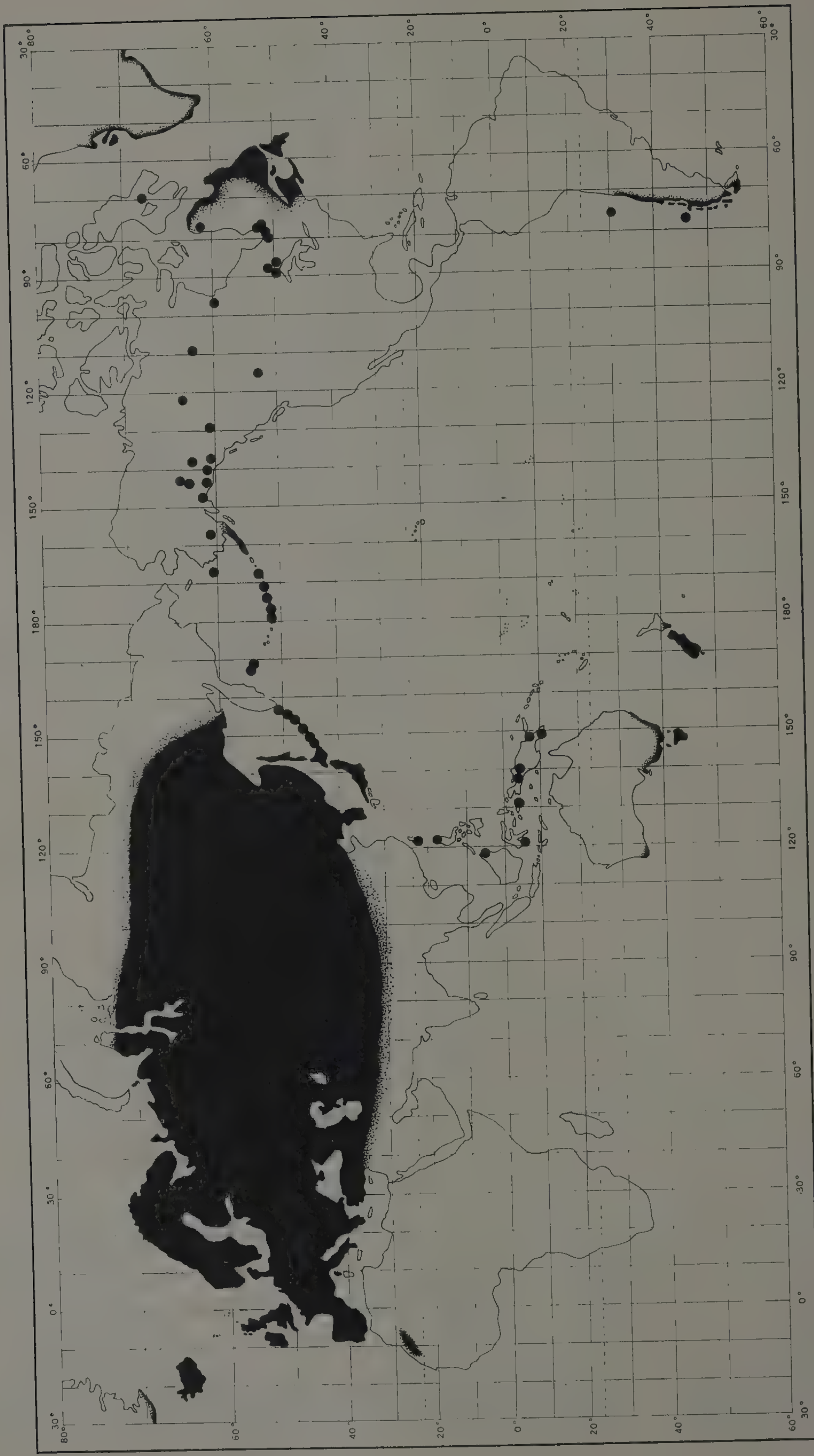
Andrews's postulated history for *Eucalyptus* is not supported by the data now available yet on the whole his idea seems to need modification rather than abandonment. The Corymbosae are probably an early type but not in the direct evolutionary line of descent; they have well-marked climatic requirements and it is reasonable to suppose that they evolved under similar conditions, but the fact that these conditions are now present in the Tropical Zone does not seem an adequate ground for placing the origin either of this type or of the genus in northern Australia. On the other hand the lack of Myrtaceae related to those of Australia in either South Africa or South America is strongly indicative of a migration of the original ancestors from the north. Furthermore he is probably correct in visualizing a northward migration by the secondary forms developed in southern Australia. On the basis of the affinities within *Eucalyptus* it is unlikely that the non-Australian species could represent primitive forms and hence suggest a non-Australian origin for the genus.

The migration from Australia of these species of *Eucalyptus* may not have taken place until the Pleistocene, during periods of union with New Guinea. It is also possible that this movement occurred at much the same time as the arrival, within the Australian Region, of the representatives of the Myrtoideae and of some of the tropical elements restricted to North-East Queensland.

While the Proteaceae may serve as an example of the affinities between southern hemisphere and Australian elements through Antarctica, and the Myrtaceae of a comparable relationship between tropical and Australian elements, a discussion of the influences revealed by a study of the Australian flora would be incomplete without comment on the presence of genera having affinities with plants of northern temperate regions. These genera include *Euphrasia*, *Stellaria*, *Ranunculus*, *Drosera*, *Hydrocotyle*, *Centaurium*, *Mentha*, *Ajuga*, and *Viola*. While southern affinities may be demonstrated for the Australian species of some of these it does not explain the presence of them all nor does it indicate the route by which there could have been interchange between northern and southern hemispheres. The best-known case is that of *Euphrasia* (Fig. 8). Du Reitz (1931, 1948) has discussed the close relationship between the Australian and Tasmanian species and those of South America but states that there is also a close affinity between the former group and the species in New Guinea. He considers that what he refers to as the "Malayan bridge" is the only route by which there could have been contact between the groups of the northern and southern hemispheres. Migration along this route would presumably have been via the Luzon and New Guinea tracks defined by van Steenis (1934*a*, 1934*b*, 1936), though the climatic regime which would have permitted such a migration is still not known. If Du Reitz's interpretation is correct then *Euphrasia* represents a palaeo-boreal element in the south.

Further information concerning the occurrence of temperate elements in New Guinea has recently been published by Hoogland (1958) in a paper on the plants of Mount Wilhelm. The assemblage he reports is an interesting mixture of northern temperate elements with southern elements such as *Drimys*, *Acaena*, *Oreomyrrhis*, *Gaultheria*, *Hebe*, *Astelia*, *Libertia*, and genera which have their major centres in the Australian Region such as *Haloragis*, *Trachymene*, and *Centrolepis*.

That communities dominated by temperate plant types occur in the tropics is well known and those in Malaysia have been discussed by van Steenis (1934*a*, 1934*b*, 1936) though unfortunately incompletely. Some comments on his papers have already been given (see Part B, Sections III and IV). Just how such communities could migrate into or through areas having a dense tropical flora and a genuinely tropical climate is by no means clear, but it is obvious that the relationship of these northern temperate elements in Malaysia and Australia requires a closer study. Not only are they linked with the recognition of important migration routes but they pose a climatological problem still unsolved. Furthermore their distribution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0°
30°

Fig. 8.—World distribution of *Euphrasia*, after Du Reitz (1940, reprinted 1948).

has some bearing on the problems relating to the stability of continental masses and the constancy of the relationships.

Undoubtedly more than one migration route if not several phases of migration are involved. Not only are there the genera quoted above, which are found in temperate habitats having a reliable rainfall, but there are also certain elements in the Eremaean flora. These too have affinities with plants in the northern hemisphere but their absence from temperate areas in Australia indicates a different arrival route or phase from that of the above genera. It is proposed to discuss some of these genera in the next section.

IV. The Origin of the Eremaean Flora

While it is not too difficult to visualize possible relationships between the floras of the Temperate and Tropical Zones with those of other parts of the southern hemisphere and of the Malaysian Region the origin of a number of the Eremaean elements cannot be as easily explained by postulating migration along the same routes, since this would involve movement of the relative communities through entirely unsuitable habitats. Nor can they be explained by deriving them from elements within the tropical or temperate portions of the Australian Region. Thus there are a number of genera, including the endemics in the Chenopodiaceae, Aizoaceae, Cruciferae, and Compositae already mentioned in an earlier discussion (see under Part A) which have definite affinities with plants of arid areas outside the Region or with plants of warm temperate areas in the northern hemisphere.

In the earlier part of this paper it was suggested that the Eremaean flora was developed from the littoral and sand dune flora of the more extensive coasts of the Cretaceous. Geologically speaking it may have been possible at this period for the communities of such sites to have received plants along coastlines linked with those of the great Tethys Sea through western Malaysia and hence there would or could have been some communication with the present Mediterranean area. Umbgrove (1930) states that the evidence indicates that there was an open sea-connection between Europe and the Malay Archipelago (Tethys) to the Cretaceous and possibly to the mid Eocene. Being based on marine deposits this leaves the question of land, or rather coast, communication still open so far as the Australian Region is concerned but it also shows that coastal continuity between Europe and Malaysia could have allowed migration of littoral communities.

Undoubtedly the greatly increased coastline of the Cretaceous, when Australia was virtually a group of islands, would have provided extensive habitats of a littoral type but the nature of the flora of such places is unknown as there are no palaeobotanical data. The chief value of an assumption of a Cretaceous arrival is that migration of coastal plants from areas to the north-west of Malaysia might have been even more difficult at later periods; but its weakness is, that had Australia received its littoral flora at such an early period one would have expected a greater development of endemic forms and a greater diffusion of such types into the Temperate and Tropical Zones. Furthermore, if the nature of the littoral flora was established at this time it must have remained in such habitats until the

Miocene at least, since with extensive development of rain-forest and other pluvial vegetation types the development of an arid flora seems improbable, though with so large a continental area rainfall cannot have been entirely uniform. It is also possible that there were littoral communities of a relevant type on the shores of the Central Australian Oligocene lake.

It is not until the late Pleistocene or early Recent that there is any real evidence for the existence of an Eremaean flora, though it was doubtless present during earlier arid cycles such as that of the early Pliocene and in the early Pleistocene. During the Pleistocene pluvial there was a great development of the primitive marsupials such as *Diprotodon* though such fauna is believed to have appeared in Australia at a considerably earlier stage. These animals were decimated as a result of the desiccation of the climate after the pluvial period, and deposits at Lake Callabonna, north of Lake Frome in South Australia, have been found to be rich in their remains. So well preserved are these that it was possible to obtain stomachic material from which fragments were determined as belonging to plants of the Chenopodiaceae and the Amaranthaceae or Nyctaginaceae (Stirling and Zietz 1900). Further information concerning deposits of a comparable age is provided by Ludbrook (1956) in a paper on the microfossils in deposits in Lake Eyre. In this case the botanical remains are limited to oogonia of *Chara* (which were also found at Lake Callabonna) and, in the more recent beds, leaves provisionally referred to the Chenopodiaceae. Since the Lake Callabonna deposits included a cone of *Callitris* in the clay containing the *Diprotodon* remains it is clear that the vegetation could have been closely similar to that of the *Atriplex–Kochia* shrub steppes which exist in the area today. Up to the present there is no evidence of the flora which must have been present during the pluvial phases, though one would anticipate that this would have included woodland and open forest types related to those of southern Australia today, since Cookson (1954) and her collaborators record many characteristic modern genera as present during the Pliocene.

Ludbrook leaves open the question whether the deposits were laid down under lacustrine or estuarine conditions though there is evidence which suggests the latter. In a footnote she mentions that an assemblage comparable to that of the Lake Eyre clays has been recovered from surface layers in swamps bordering Lake Alexandrina, i.e. the dune-enclosed waters at the mouth of the River Murray. Estuarine conditions would have provided an excellent route by which littoral plant communities could have penetrated deep into the continent. In these sites they would have been isolated from coastal areas by a later fall in ocean level. The recent history of the Lake Eyre basin involves deflation of the lake surface and the development of extensive dune systems under arid conditions (Crocker and Wood 1947; King 1956). Consequently, despite the later pluvial stages in the post-Pleistocene period and the isolation of the old estuarine (?) communities far from coastal areas, there would have been suitable habitats in which modification into the modern Eremaean forms could have occurred. It may be significant in this connection that a number of the endemic and characteristic genera of the families mentioned above have centres of development, if not of origin, in the arid portions of South Australia. There may have been other suitable habitats resulting from the drying-up of the many lakes of the pluvial phases. These included Lake Dieri in South Australia, which covered the area of the present Lake Eyre and others in the same area, and Lake Nuwait in the south-west of New South Wales and the north-west of Victoria. The now dry "lakes" of Western Australia may also provide us with further information concerning the development of the Eremaean flora if deposits in them prove deep.

It may be possible to correlate this postulated history for certain elements of the Eremaean flora in the Lake Eyre region with the history given by Crocker and Wood (1947). They visualize an earlier flora which was destroyed, or at least decimated, by conditions during a Great Arid Period. This Great Arid Period may have been that now believed to have occurred at the end of the Pleistocene though at present it is not possible to distinguish between the effects of the various arid cycles which have occurred. These authors consider that, following the destruction of much of the vegetation of Central Australia during the dune forming stage, the area was chiefly repopulated by species which had survived the adverse conditions in refugia. One can hardly doubt that this would have been the case in many genera but the facts given above show that the recolonizing elements included some which cannot have come from the sclerophyllous types of the temperate areas, or from the tropical north. Since many of the special elements are ephemerals it seems probable that they were able to persist even during the most arid stages by occupying suitable habitats in the vicinity of scattered and temporary waters.

The arid period of the late Pleistocene or early Recent, whether it should or should not be regarded as a "Great Arid Period", was followed by at least two pluvial phases which were separated by further arid cycles and followed by another which is still in progress. During the pluvial phases the climate was sufficiently wet to permit the formation of laterite over wide areas of the continent (Jessup, unpublished data). At present the relative importance of the various dry and wet phases, so far as phytogeography is concerned, is not understood. We are unable to separate the effects of the different stages of each climatic type until the various intensities of the oscillations and their chronology is better known. Without doubt there has been a succession of retreats and advances in a more or less concentric fashion as the climate became alternately drier or wetter. In each case the "Australian" sclerophyllous type in the south and the "tropical" type in the north and east has retreated before increasing drought and advanced with increasing rainfall. These retreats have left clues in the distribution patterns discernible today but it is the correlation of particular discontinuities with definite phases of climatic conditions that is obscure.

Another effect of climatic oscillations has been that of the stresses developed along the junction between major floristic types. The high degree of specific variability to be found in Interzone 1 at the junction of the South-West Province and the Eremaea has already been discussed under "South-West Province" (see Figs. 2 and 3). These stress areas are also indicated by the peripheral groupings of localized species in several genera, e.g. *Swainsona* (Lee 1948) and *Triodia* (Burbidge 1953). Other areas where a high degree of variability or local endemism may be related to such effects are the MacPherson–Macleay Overlap, and the Hamersley Range in Western Australia (Burbidge 1959). It is probable that stresses have been high in these areas in each of the arid phases since the Pleistocene and we cannot, therefore, expect to be able to distinguish between the effects of the different phases in these areas until a great deal more data become available. At present it is necessary to depend on more marked discontinuities between and within the main zones.

With the return of pluvial conditions after the earliest of the arid periods under review it is probable that the winter rainfall system influenced a greater area of southern Australia than it does today. This inland movement of the rainfall belts would have allowed not only some west–east interchange but also a northward migration of southern elements. This may explain the presence, in Central Australia, of such species as *Hakea multilineata* Meissn. and *Burtonia polyzyga* (F. Muell.) Benth. in the MacDonnell Range and isolated occurrences of mallees such as *Eucalyptus oleosa* F. Muell. Also, since there is no evidence that the pluvial phases were limited to southern Australia, it may be supposed that the northern areas were similarly wetter than at the present time. This would have greatly restricted areas suitable for Eremaean elements but it would have permitted a southward migration of tropical species. A possible example of these would be *Livistona mariae* F. Muell., now isolated far from other palms, in the MacDonnell Range refugium. Another would be *Erythrina vespertilio* Benth. whose distribution includes scattered colonies as far south as Oodnadatta. A less definite case may be the southern occurrences of *Eucalyptus* spp. of the Corymbosae type of which two or three are to be found in Central Australia. That both northern and southern areas were pluvial at the same time is indicated—though not proved—by the fact that the flora of the northern Eremaea is not nearly so rich in distinctive elements as the south. Had the Eremaean flora of the arid period (Great Arid Period?) been pushed north by a southern increase in rainfall one would have expected to find local species of the southern Eremaean types but these are comparatively rare and the genera are commonly represented only by widespread species. The flora of the northern Eremaea is dominated by species with tropical affinities adapted to tropical but arid conditions. It is of course possible that an earlier flora, of a southern Eremaean type, has been eliminated during a more recent phase but this seems improbable owing to the relict distribution indicated by the above quoted species and is not indicated by the pedological data.

Since the history of the Eremaea is so closely related to climatic variations since the Pleistocene it is advisable to consider it in association with the possible development of some of the flora of the present-day Temperate Zone. The most crucial, since the most vulnerable, area is that now within the Temperate Zone in South Australia. Following the return of pluvial conditions (and if the aridity is assumed to have been so severe as to eliminate most of the southern sclerophyllous type) this part of South Australia would have been repopulated from refugia in the Flinders Range or Mt. Lofty Range or from areas to the south-east where, owing to climatic gradients, the effects of aridity would have been less. That there was an arid period of greater effective intensity than that of the present time is clearly indicated by the very extensive dune systems of Central Australia (Crocker and Wood 1947). For this reason a stage in which almost the whole of South Australia must have carried meagre but Eremaean-type vegetation seems unquestionable. The real problem is, from whence was the southern portion of this area repopulated? That migration from east or south-east could have occurred, is indicated by the strong affinities between the modern flora of temperate South Australia and of Victoria and eastern Australia. In contrast to this, the number of western species is very low and in several cases their occurrence is limited to Kangaroo Island where survival might have been favoured by the coastal climate. Nevertheless, though the affinities with the flora of Victoria are so strong, the relationship is not a simple one.

Recent work on *Themeda australis* (R. Br.) Stapf by Hayman (1960) has shown that there is a tetraploid population in the Mt. Lofty Range, similar to that of northern Victoria and western New South Wales. This race is geographically distinct from the diploid populations of southern Victoria and eastern New South Wales. If one assumes that the South Australian area was partly repopulated from the south-east then one would have expected to find the diploid present, especially since its occurrence in Tasmania indicates that it was in south-eastern Australia prior to the final separation of the island from the mainland in the late Pleistocene. The diploid is not found in Western Australia and hence there is no evidence that it was ever widespread in southern Australia.

During the Pleistocene the Murravian Gulf, which had persisted from Miocene times, was greatly reduced in area by the uplift of the Mallee Ridge (Browne 1945) with the result that Lake Nuwait was dammed back to the north and north-east until the ridge was cut by the Murray River. Until this formation of Lake Nuwait, which Browne places in the pluvial phase of the Pleistocene but prior to the later uplift phase in the Spencer and St. Vincent Gulf areas, the modern Mt. Lofty Range area would have been isolated from southern Victoria. Interchange of biotypes would have been handicapped by the necessity of migration around the northern shores of either the Murravian Gulf or, at a later stage, those of Lake Nuwait. This would have involved passage through inland areas which may well have had a lower rainfall. On the other hand, during a pluvial phase the flora around the lake would doubtless have been comparable with that occurring in more southern localities today. At the onset of severe aridity the receding of the lake waters would have left habitats suitable for Eremaean elements, and southern elements may have been destroyed. It is also possible that, if not already continuous, the flora near the lake would have retreated towards the Mt. Lofty and Flinders Range areas. Another retreat route would have been into southern Victoria.

During later pluvial phases there should have been some reoccupation of the vacated area and this, with a corresponding expansion in the South Australian area, could have led to an interchange of biotypes. This advance would, however, have been influenced by the fact that Lake Nuwait was not reformed owing to the drainage resulting from the development of the Murray River and also by the extension of the coast by a series of strandlines which advanced the land area about 50 miles further west (Crocker and Cotton 1946). Such physiographic changes must have affected the extent to which rainfall belts would influence inland areas. Whatever the effect of this in a pluvial phase might have been, the fact that today there is a prevalence of mallee and heath type associations in this area between temperate South Australia and the Grampians in Victoria shows that during the current arid phase little interchange is possible.

If the Murravian Gulf and Lake Nuwait did form a barrier between South Australia and southern Victoria until the late Pleistocene, then it is possible that the former may have had a flora with much in common with that of the South-West Province, at least prior to the worst arid phase. This might well have been so since there are indications that the Nullarbor Plain may not have been the edaphic barrier that it is today (Jessup, unpublished data). In other words it may be postulated that until the "Great Arid Period" which saw the formation of the great dune systems and the removal of the soil from the Nullarbor there was no real barrier to prevent continuity between the flora of south-western Australia and that of South Australia. Once the Nullarbor became a barrier then such continuity was impossible, and migration could only take place through inland, and presumably drier, areas. Movement along such routes may explain the occurrence of western species such as *Hakea multilineata* in Central Australia and possibly the spread of the mallee type of *Eucalyptus* into Eastern Australia, but the elements now so characteristic of the South-West Province would have been effectively isolated. For this reason it may be suspected that the occurrence of such western elements as *Adenanthos*, *Thomasia*, *Trymalium*, and *Marianthus*, all of which are represented by few species in South Australia and western Victoria, may be relict in nature.

If the South Australian temperate areas were repopulated, at least in part, by elements previously associated with the Lake Nuwait area then the presence of the tetraploid race of *Themeda australis* can be explained but this leaves unanswered the query why a similar retreat into southern Victoria did not take the tetraploid race into the diploid area. It is known that the Dividing Range in Victoria is an important barrier to plant migration, but whether this is a factor in the present case is still obscure. As a species *Themeda australis* has an extraordinarily wide climatic range. It occurs from the savannahs of northern Australia to the cool temperate conditions at 4000 ft in the Australian Alps. It may be found along dry water courses in the arid areas of Central Australia or in high-rainfall areas in eastern Australia. There is, therefore, no obvious reason why the races in temperate South Australia and southern Victoria should differ cytologically and according to a definite geographic pattern. This problem, posed by *Themeda australis*, makes it clear that a close analysis of the flora of temperate South Australia and of southern Victoria would be a profitable phytogeographic study. It is not impossible that the affinities, or conversely the lack of affinities, between the plants of these areas will prove as significant to our understanding of past floristic changes as may those of the flora of the MacPherson–Macleay Overlap. This opinion, based on the botanical situation, is supported by the fact that Tindale (1949) was unable to relate the distribution of certain butterflies in the south-east of South Australia with the possibility of the area having been affected by Crocker's and Wood's Great Arid Period. It is obvious that we need to know much more about biological interrelationships as well as about climatic oscillations in this area since the Pleistocene.

Apart from the discontinuities which indicate past climatic and floristic changes the flora of the Eremaea has certain features which suggest that many of its characteristic elements may be of relatively recent development. The flora exhibits a curious mixture of uniformity and variability. Thus the species *Acacia aneura* F. Muell. (mulga) occurs throughout much of the southern and central portions, especially where the rainfall varies in both annual volume and seasonal occurrence. The general representation of species in association with it changes comparatively little over many hundreds of miles. *Acacia aneura* itself shows a great deal of variability in growth habit and in phyllode dimensions but the minor forms not only re-occur in many localities but re-occur in association with one another. There is little evidence that the forms can be subdivided into geographic races though it may be possible to recognize a series of ecotypes. Variation in other plants, whether species or genera, is present but it is significant that it is workers who have not seen the plants in the field who have attempted to separate them into distinct categories. Thus Ulbrich (1934) considered that the Australian taxa should not be retained in the Mediterranean and northern genus *Bassia* All. (Chenopodiaceae) and he proceeded to distribute the Australian species among no less than six genera, of which three are monotypic and one ditypic. Similarly Schulz (1936) divides the species formerly included under *Blennodia* (Cruciferae) into a number of small or monotypic genera. The fact that the recognition of these minor groupings involves the employment of microscopic characters suggests that the taxa may not be old enough to have become well separated at the generic level.

The affinities of these Eremaean representatives of the Chenopodiaceae and Cruciferae seem to lie with taxa of the temperate areas of the Old World. Other examples include *Atriplex* and *Kochia* (Chenopodiaceae), *Hymenolobus*, *Phlegmatospermum*, *Blennodia* s.s., and the Australian Cruciferae placed in the subtribe Arabidopsidinae by Schulz. Van Steenis's study of the temperate genera present in the mountain flora of Malaysia has shown the difficulties which oppose the transit of temperate elements through a tropical area but a route via littoral habitats appears possible so far as the Australian representatives in the Eremaea are concerned. In this connection it is interesting to find that genera regarded as typically Eremaean in Australia, such as *Ptilotus*, *Tetragonia*, *Trianthema*, *Tribulus*, and *Salsola* are found either in coastal habitats or restricted to low altitudes in Malaysia today (see *Flora Malesiana*). It thus appears likely that the temperate elements which have developed into the Eremaean types of today may have followed a different route from the northern hemisphere than that which may have been travelled by other northern temperate elements such as *Euphrasia*, *Viola*, and *Ranunculus*.

V. Plant Migration Routes and the Tectonic History of Australia

The tectonic history of the Australian Region as discussed in the Geology of the Commonwealth of Australia (David 1950) offers some interesting possibilities so far as plant migrations in the past are concerned. In Chapter XV, there are a number of diagrams illustrating the position of the major geosynclines (Figs. 9, 10, and 11). From the Cretaceous to the Miocene the continent is shown as lying between the Westralian Geosyncline (with possible land areas in the present Indian Ocean), the Tasman Geosyncline (with "Tasmantis" between the sunken area and New Zealand) and the Papuan Geosyncline with an extension of the sunken area between New Guinea and New Zealand. The continental mass is indicated as being little larger than at present but the area of Tasmantis may have extended further south. Tasmania was continuous with the continental area and the land surface extended further south than it does at present. This ancient geography is necessarily largely hypothetical and it is clear from the remarks of Glaessner (1952) that it is not entirely supported by certain geological evidence now available, at least for the period of the Tertiary. Nevertheless certain matters arise from the discussion which are of considerable importance for the phytogeographer. It would appear, for example, that there has long been some form of sea barrier between eastern Australia and New Zealand but this barrier may have been less important in the Coral Sea area. If this was so then interchange of taxa between north-eastern Australia, New Guinea, New Caledonia, and New Zealand would have been

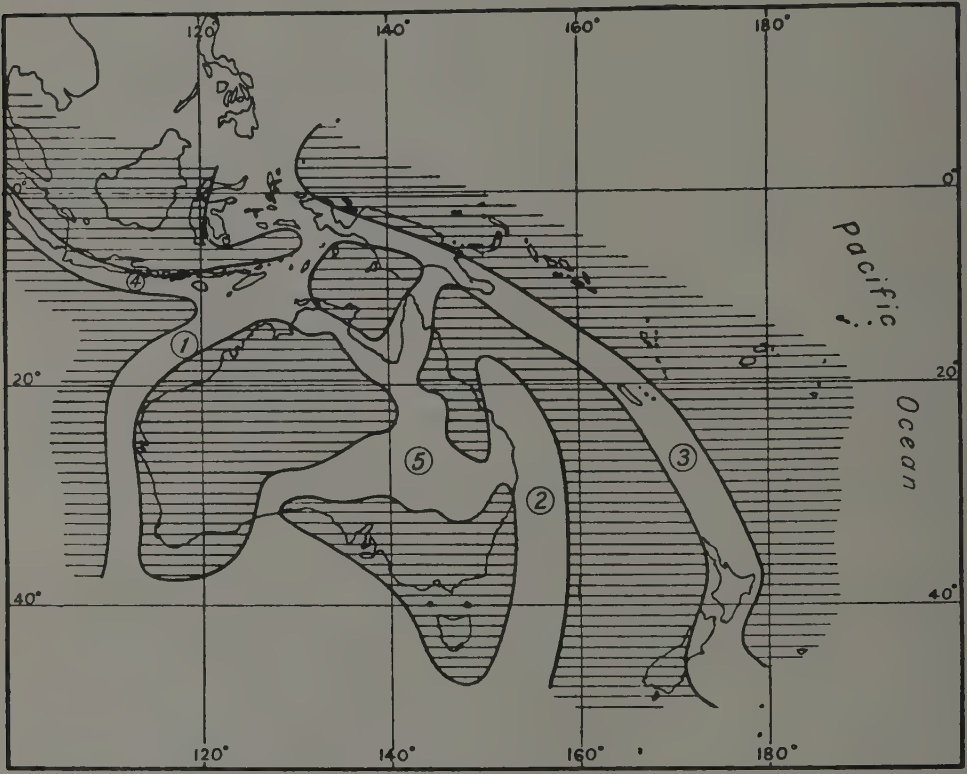

Fig. 9.—Westralian (*1*), Tasman (*2*), and Papuan (*3*) Geosynclines in Aptian time, with the Roma Epeiric Sea (*5*), showing probable connections with each other and with the Timor–East Celebes Geosyncline. (After David (1950).)

more possible than it is today. This leaves open the question concerning the curious links between the flora of New Zealand and Tasmania, which may be linked with some southern route not related to the movements that occurred along the branches of the New Guinea track. It may be significant that the few representatives of the Myrtaceae–Leptospermoideae present in New Zealand are genera which also occur in New Caledonia and New Guinea while those of the Epacridaceae may either be related to the northern route or are shared with Tasmania and south-eastern Australia. Since, however, the Epacridaceae appear to be a southern family it may be suggested that they should be regarded as palaeoantarctic elements in their northern occurrences. If this is correct then it is curious that they have not been recognized in early Tertiary deposits.

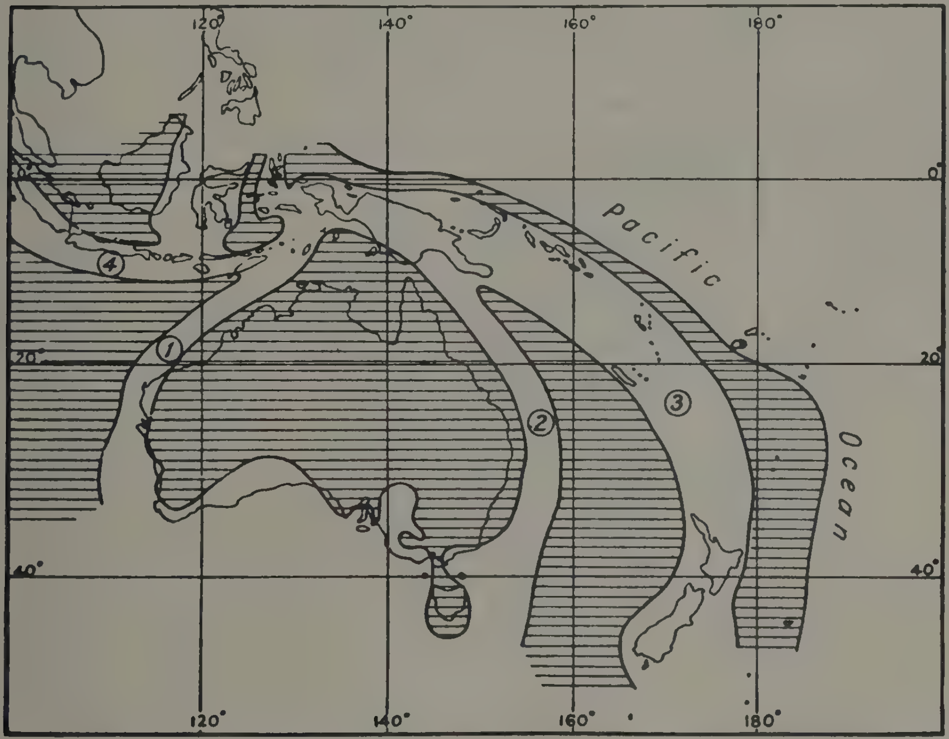

Fig. 10.—Westralian (*1*), Tasman (*2*), Papuan (*3*), and Timor-East Celebes (*4*) Geosynclines in Eocene time. (After David (1950).)

In the north the geological evidence, though not entirely satisfactory, suggests that contact with the Asian area might have been possible up to the late Cretaceous or early Tertiary, or at least there would have been periods when migrational advances on the intervening land surfaces might have permitted migration into or out of the Australian Region. During the early Tertiary the two areas were separated by the Timor–Celebes Trough but since much of the Sahul Shelf may have been exposed in part or as a whole, at different times, the northward extension of the continent would have reduced the effect of the oceanic barrier. Fairbridge (1953), in a study of the Sahul Shelf, makes it clear that the Wegenerian idea of an Australian land mass drifting north to impinge on the Indonesian area in the Mesozoic or Tertiary is geologically untenable. Certainly such an idea creates even more problems than it solves so far as it concerns the affinities of the elements of the Australian Tropical Zone or of tropical elements in southern areas with those of the islands of the Near North. On the contrary these are too numerous to make such a hypothesis even desirable.

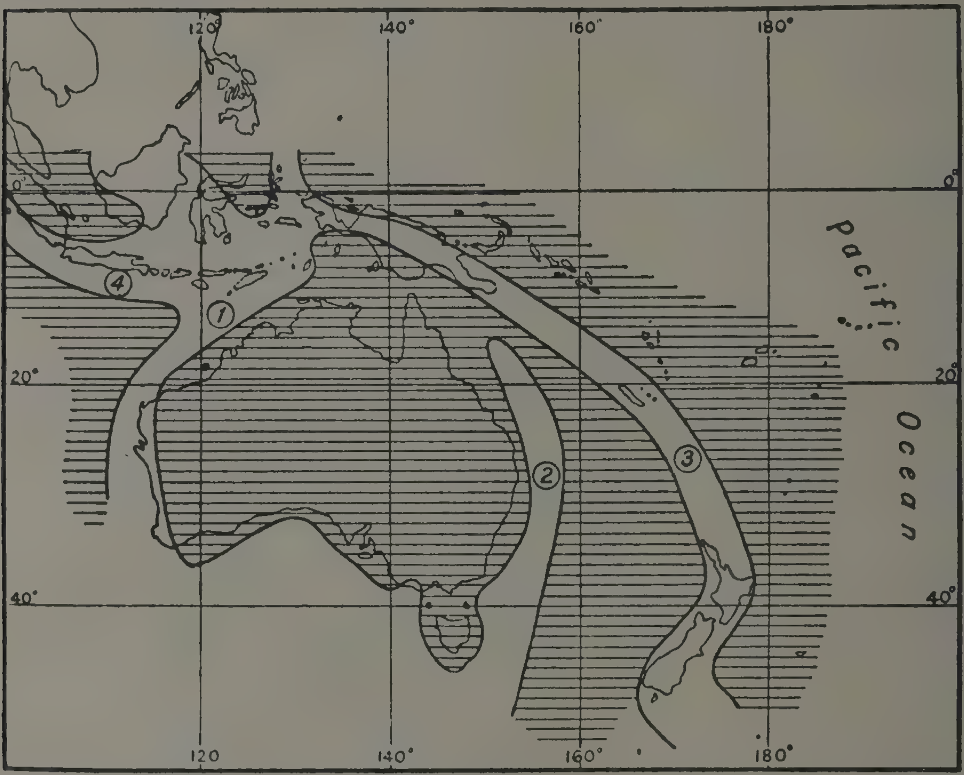

Fig. 11.—Westralian (*1*), Tasman (*2*), Papuan (*3*), and Timor–East Celebes (*4*) Geosynclines in Miocene time. Note that the Australian Continent is completely ringed by seas, includes part of New Guinea, and has the Nullarbor and Murravian shelf-seas. (After David (1950).)

If some form of communication between the Australian Region and western Malaysia, i.e. the portions to the west of Wallace's Line, was possible prior to the Tertiary then it may explain the presence of some of the tropical elements in the Cinnamomum flora and also the representation of certain temperate genera, particularly in the Eremaea. The alternative is to suppose that these reached Australia by advancing from island to island through eastern Malaysia and from thence to Australia via some portion of the Sahul Shelf or through New Guinea. Doubtless this eastern route has been important but it has not necessarily been the only one, so far as the earlier migrants are concerned. Furthermore these earlier migrants must have reached the Australian Region long before eustatic lowering of sea-level exposed inter-island areas in both western and eastern Malaysia during the Pleistocene.

New Guinea must have been a crossroads for migrations during much of the Tertiary. Not only was there the link with Australia but movement to and from New Caledonia and New Zealand may be presumed (see Table 7). It was also a focus on the migration routes from Western Malaysia and the Philippines even though passage was restricted by the Sunda Deep (Fig. 12). The route to New Zealand may have persisted until the Pliocene. Fleming (1944), on the basis of changes in fossil Mollusca, states that the seas around New Zealand were colder in the early Pliocene than in the late Pliocene or Pleistocene despite the cooler climate of the latter. This relative warmth of the New Zealand seas has persisted until the present day. He relates this to the presence of the Notonectian Current which, arising as a southern branch of the South Equatorial Current, sweeps past New Caledonia, down the east coast of Australia and then turns east to New Zealand. It will be evident that such a current could only exist if there was no barrier to its passage along this route and it follows that its apparent non-existence in the earlier periods indicates the presence of such a barrier. Hence there may have been a land connection mass or a more complete island chain in the Tasman Sea which prevented the current from reaching New Zealand.

It is interesting in this connection to consider the affinities of the flora of Lord Howe Island which lies in the Tasman Sea almost equidistant from Australia, Norfolk Island, and New Zealand though nearest to the first area. It is situated on much the same latitude as Port Macquarie, i.e. about level with the southern area of the MacPherson–Macleay Overlap.

Its flora and fauna have been recently discussed briefly by Paramonov (1958) but the most detailed account of the flora is still that of Oliver (1917). Unfortunately this is now out of date both taxonomically and nomenclaturally and a re-examination of Oliver's material and further collecting would be necessary before a critical comparison of the affinities with the flora of Australia or New Zealand could be made. However, despite this qualification, Oliver's list reveals certain peculiar and significant features which are more likely to be verified than altered by such re-examination. According to his catalogue the angiosperm flora includes representatives of 66 families, 137 genera, and 159 species. The majority of the genera are represented by a single species and none has more than three species. The Proteaceae are not represented. The Leguminosae include a *Caesalpinia*, a *Sophora*, one genus of the Galegeae, and three of the Phaseoleae. The Myrtaceae are represented by *Metrosideros*, *Leptospermum*, and *Melaleuca*, all in the Leptospermoideae, the first having an important centre in New Zealand and all occurring in Malaysia. The Epacridaceae are poorly represented.

The wide family representation and the relative lack of special development within any particular family or genus suggests that the flora must be considered as having been isolated in comparatively recent times. The development of the Notonectian Current may indicate that the land mass represents a fragment developed as a result of the breakup of Tasmantis, but Glaessner's (1952) suggestion that it appeared following volcanic activity in the late Tertiary is probably the more likely. In this case the origin of its flora remains a problem.

In some cases Oliver refers the local material to an Australian species. All these must be regarded as requiring verification though doubtless some may be correctly placed. At the generic level the relationships are of considerable interest. As noted by Paramonov a majority of them also occur in Australia but, significantly, the larger number are genera with tropical affinities. Within the Australian Region they are mainly found in the Tropical Zone, especially in eastern Queensland and the MacPherson–Macleay Overlap. Furthermore the great majority have also been recorded from New Guinea and New Caledonia as well as from New Zealand. There is, therefore, little to suggest that they have migrated from Australia, unless it was by an indirect route. There are, however, some genera which cannot be as readily referred to the branches of the New Guinea track. These include *Drimys* (Winteraceae) an Antarctic element though it reaches New Guinea, *Hymenanthera* (Violaceae) otherwise limited to New Zealand and to elevated areas in Tasmania and south-eastern Australia, *Pimelea* (Thymelaeaceae) of which the single species is referred to subsection *Eupimelea* and hence to a distribution similar to that of *Hymenanthera*, and finally *Westringia* (Labiatae) otherwise limited to Australia. In this last case *W. rosmariniformis* Sm. is a coastal species common near Sydney and its indigenous occurrence on Lord Howe Island may be open to doubt. There are also a number of littoral species whose extensive distribution in coastal habitats makes them less satisfactory indicators of floristic relationships. These include *Rhagodia baccata*, *Atriplex cinerea*, *Salicornia australis*, *Tetragonia* spp., *Mesembryanthemum* spp., *Myoporum insulare*, and *Scaevola frutescens* (all sensu Oliver).

Further consideration must be left until the flora has been more critically examined in the light of modern knowledge of Pacific floras. At the risk of over-simplifying the situation it may be summed up as follows. The strong representation of genera which, though in Australia or New Zealand, occur in New Guinea, Malaysia, and other northern areas makes it difficult to suggest the route by which they arrived. The existence of affinities with south-eastern Australia, Tasmania, and New Zealand suggests that more than one floristic element is present. There is no indication that the island has ever been directly connected, phytogeographically, with eastern Australia within the period under discussion.

Under the "glacial" climate of the Pleistocene the Notonectian Current would doubtless have had an ameliorating effect on the climate of coastal areas of eastern Australia. It would have created conditions favourable to the extensive occurrence of fogs and other high humidity states favourable for rain-forest development whether of temperate or tropical type. Conversely under "interglacial" conditions with a warm dry land area and a warm sea current the ranges of eastern Australia may not have been sufficiently high to force the loss of rain from passing cloud systems. One would expect that only the coastal fringe would enjoy a mild wet climate and that there would have been a very arid rain-shadow to the west of the ranges. Nevertheless it is improbable that the well-marked eastern Australian migration route has ever been as seriously interrupted by climatic change as is the corresponding western route between the Tropical and Temperate Zones in Western

Australia under current conditions. The degree of the interruption in the eastern route is indicated by the discontinuities now existing between North-East Queensland and the MacPherson–Macleay Overlap and discussed in the section dealing with the latter.

Keeping these facts in mind it is interesting to consider the distribution of certain plants commencing with the Liliaceae.

The genera placed under the Liliaceae in the early tables of this account are those included within the family by Krause (1930), but for distribution analysis it is instructive to arrange them in accordance with Hutchinson's system (1934). The majority of those in the Australian Region occur in the Temperate Zone but dealing for the moment with those found in both Tropical and Temperate Zones within the Region it is found that there are 11 genera which, under Hutchinson's arrangement, are grouped as follows:

Liliaceae:	Asphodeleae:	*Chlorophytum*
	Dianelleae:	*Dianella*
	Uvularieae:	*Schelhammera*
	Johnsonieae:	*Borya, Sowerbaea, Tricoryne*
Philesiaceae:	*Geitonoplesium, Eustrephus*	
Xanthorrhoeaceae:	*Lomandra*	
Smilacaceae:	*Smilax, Ripogonum*	

Of these the Johnsonieae are all Australian endemics since the tribe is restricted to the Region and has its main centre in the South-West Province. The Dianelleae are represented in Australia by *Stypandra* as well as by *Dianella* and the latter genus is also found around the arc of the Near North from the Mascarenes through tropical Asia to New Zealand. It is also in Hawaii. Curtis (1952) reported that there is evidence of both auto- and allopolyploidy in the Australian species. She reports a number of high chromosome numbers from Tasmanian material and these may be contrasted with a diploid recorded from New Zealand (Hair 1942) and a tetraploid count for *D. ensifolia* Red. Lil., which is also found in Asia and Hawaii as well as in Australia. *Dianella* appears to be a very old resident in the Australian Region and there has been some special development in Tasmania. Of the other genera listed by Hutchinson under the *Dianelleae*, *Excremis* is South American, and *Walleria* is from tropical Africa. There is a possibility that the tribe is a very old southern one.

In the Uvularieae (where *Walleria* is again listed) there is a group of southern and tropical African genera. *Gloriosa* extends from Africa to tropical Asia, *Uvularia* is North American, and *Schelhammera* and *Kreysigia* are Australian but limited to eastern localities. Whatever may be the centre of origin of this tribe it is probable that the Australian representatives are comparatively late migrants from the north.

Under the Asphodeleae the genera *Hodgsoniola*, *Chamaescilla*, *Agrostocrinum*, *Corynotheca*, *Dichopogon*, and *Bulbinopsis* are endemic to the Australian Region and almost wholly limited to the Temperate Zone. *Caesia* is also represented in South

Africa, *Herpolirion* is monotypic and limited to high elevations of south-east Australia, Tasmania, and New Zealand, *Arthropodium* (with which *Dichopogon* should perhaps be included (Payens 1957)) also occurs in New Guinea. *Thysanotus* extends north to China but has an important centre of development in the South-West Province. Hutchinson regards the tribe as primitive within the Liliaceae and it has a world-wide distribution though the majority of genera appear to be in the southern hemisphere. Wherever the tribe may have originated it would appear that *Arthropodium* and *Thysanotus* may be Australian elements and that they should be recognized as such where they occur outside the Region. *Herpolirion* is an example of the Tasmanian–New Zealand linkage which appears independent of the northern route. On the other hand *Chlorophytum* has the majority of its species in tropical Africa and it may be regarded as a migrant from the north within the Australian Region, where there is one non-endemic species that reaches northern Australia and one endemic species limited to Tasmania and to high elevations in south-eastern Australia. It would be interesting to know the cytotaxonomic relationship between these two species and between them and the two South American ones. At present it may be suspected that the local species belong to different lines of descent and to different periods of arrival in the Australian Region.

For the other cases the Philesiaceae may have had an Antarctic or southern origin but the Smilacaceae appear to be northern. The occurrence, in northern and eastern Australia, of *Smilax* and *Ripogonum* may be related to ancient connections with lands to the north and with the north-eastern junction with Tasmantis to which latter route we also refer *Lomandra* though, as the remainder of the Xanthorrhoeaceae are Australian endemics, the tribe should be regarded as an Australian element.

The distribution of the Proteaceae has already been discussed but their scarcity in New Zealand, if they had an Antarctic origin, is peculiar. The Proteaceae are always closely associated with species assemblages in which the Leguminosae–Podalyrieae are well developed (at least so far as Temperate Zone localities are concerned) and the absence from New Zealand of this tribe as well as of most of the Proteaceae may be due to the same cause. In other words, it may be that neither along the north-eastern route nor through a southern route were the climatic conditions suitable for migration of communities dominated by such plants. It is curious that of the two Proteaceae in New Zealand one, *Persoonia toru* A. Cunn., falls in the same section as *P. falcata* R. Br. which is the only member not only of the genus but also of the subfamily to reach northern Australia, while the other, *Knightia*, is related to *Darlingia* which is endemic and restricted to north-east Queensland. The fact that *Knightia* also occurs in New Caledonia increases the probability that these plants reached New Zealand by the northern route and it may be significant that Oliver (1953) does not report *Knightia* as present in New Zealand until the Pliocene—much later than the Proteaceae first appeared in Australian Tertiary deposits. Cockayne (1958, p.422 *et seq.*) in outlining the possible history of the New Zealand flora recognizes a "Great New Zealand" period of the Cretaceous and early Tertiary with important development of palaeotropical elements and probable connections with Norfolk Island, the New Hebrides, New Caledonia, New Guinea, and northern Queensland (i.e. presumably via the northern areas of Tasmantis). These northward affinities were associated with invasions from the southern Antarctic. During the Oligocene–Miocene the land area was greatly reduced, though there may have been other land surfaces at no great distance, and the flora must have been greatly reduced in representation. He considers that further invasions from the south are unlikely in the Pliocene–Pleistocene when elevation of the land recommenced but it is difficult to account for the close relationships at the specific level between Tasmania and New Zealand if this was so. However since these affinities concern plants with cool climate requirements it is unlikely that the Proteaceae could have followed such a route, especially when it is recalled that the Grevilleoideae lack restricted endemics in Tasmania, an absence that may have resulted from destruction of local types during the Pleistocene cold phases.

As has already been discussed, Australia shares a number of proteaceous genera with South America (Fig. 6), there being closer affinities in this case than between Australia and New Zealand or between Australia and South Africa. The lack of close affinities with the flora of South Africa is most marked, especially in view of the opinions expressed by some authors, though Good (1953) emphasizes the parallelism rather than the affinities between the flora of the Cape Peninsula and that of the South-West Province of Western Australia. The lack of affinities at the generic level is also revealed by a critical phytogeographical analysis of the Cape Peninsula flora by Weimarck (1941) who lists only four genera which also occur in Australia. These are *Restio*, *Leptocarpus*, *Hypolaena* (Restionaceae), and *Caesia* (Liliaceae). Even in these cases the lack of affinity is emphasized by the fact that the inclusion of the first three is dependent upon the acceptance of the congenericity of the South African and Australian species. Weimarck deals mostly with the possible history of the flora during the Quaternary and no special details concerning the pre-Quaternary climates or flora are given. He regards the Cape "endems" as relicts and considers that their survival is due to their adaptation to a climate with winter rain and summer drought. Such a conclusion further emphasizes the developmental similarity between this flora and that of the South-West Province where many of the endemic genera and species are similarly considered to be relict in nature. An analysis of the affinities between the South African flora and that of the South-West Province has been given by Gardner (1944) who also found that the affinities with South America are stronger than those with South Africa. He, too, mentions the fact that the tribe Podalyrieae of the Leguminosae is found in South Africa and Australia but is absent from New Zealand and South America. In view of the ecological association of these with the Proteaceae in many plant associations throughout the Temperate Zone, this relationship should be remembered when the possible origin of the Proteaceae is under consideration.

Just as the Tasman Geosyncline was a barrier which prevented interchange between eastern Australia and New Zealand except by indirect routes so in the west was the Westralian Geosyncline a barrier which prevented interchange between the southern areas of Africa and Australia. Nevertheless the geological evidence seems to favour the existence of a land area in the present Indian Ocean and it is interesting to speculate whether this provided the route by which *Adansonia* came to occupy its present area with species in tropical Africa and Madagascar and a single representative in the Kimberley Division of Western Australia. This possibility may also explain some of the curious relationships between the floras of Madagascar and Australia. These are mentioned by Good (1950) in his discussion of the floristic affinities between Madagascar and New Caledonia. Examples he quotes include *Albizia*, *Grewia*, *Pittosporum*, *Myoporum* (Mauritius), and *Dianella* to which may be added the data on the distribution of *Dillenia* provided by Hoogland (1952). In all these cases the line of distribution Madagascar–Malaysia–New Caledonia would be less disjunct if there was a possible connection in the past through the Indian Ocean and Australia. Nevertheless while the geosynclinal features of Australia may help to explain these discontinuities it must be kept in mind that the accumulating data on polar movements may also contribute to the solution of such problems of distribution. If polar movements were the result of continental movement then it may still be necessary to accept some of the proposals dealt with by the Wegenerian supporters even though the evidence clearly shows that the affinities between the Australian flora and that of Malaysia are too close for complete acceptance of the hypothesis as it stands.

This relationship with areas to the north of the Region is further emphasized when cosmopolitan groups are considered. For example under the cosmopolitan genus *Carex* (Cyperaceae) Nelmes (1942–43) lists 45 species for Australia. The majority of these are found in eastern Australia but the affinities reveal that some are close to if not conspecific with European species, others are conspecific with, or related to, Asiatic species, and a small group has affinities with species in New Zealand and South America. Nelmes accepts the view of Kreczetowicz that *Carex* probably had a Malayan origin. If this is so then there is additional evidence concerning the importance of the eastern migration route as a path between the lands of the Near North and ancient Antarctica. This path has also, according to Du Reitz (1931), been followed by *Euphrasia*.

In the case of the Rubiaceae, another cosmopolitan group of great antiquity, some information concerning the distribution of tribes has been given by Verdcourt (1958). From this it is evident that the majority of the Australian affinities lie to the north, i.e. with taxa in Asia, Malaysia, or Polynesia. Affinities with New Zealand representatives are not numerous though one example is *Coprosma*. As may be seen from Table 2 the majority of the Australian genera are restricted to the Tropical Zone and to the MacPherson–Macleay Overlap. Few are to be found in the South-West Province and the genera occurring in the Eremaea are generally limited to a few widespread species. In neither of these zones are there rubiaceous restricted endemics. Some genera, such as *Asperula*, *Galium*, *Opercularia*, and *Coprosma*, are represented by species in eastern Australia and Tasmania but in none of these cases is there more than a few species. Thus, while the possibility of some of the taxa representing southern migrants cannot be wholly ignored, the indications are that they are tropical elements which have entered from the north and which have advanced mainly along the eastern route. The fact that some genera do not occur south of the MacPherson–Macleay Overlap suggests that they may have had a wider distribution in earlier warmer and more pluvial periods.

During such periods or during the early Tertiary period of warmer climates the few representatives in the South-West Province and the Eremaea may have been able to migrate into their present areas. A later period is the more likely owing to the lack of western endemic genera and the presence of affinities at the specific level. On current distribution the main centre within the Australian Region is in the north and north-east but possibly the lack of endemics in the South-West Province is due either to a late Tertiary migration or it may be related to ecological factors concerning the lack of warm season precipitation and the occurrence of a marked summer drought.

From Table 3 it may be seen that in the Temperate Zone genera having tropical affinities account for nearly a third of the total. Some of the "tropical" elements may, in fact, be palaeoantarctic in origin but they all have a wide distribution in Malaysia and some occur in tropical Asia and tropical Africa. Such a distribution in tropical areas and throughout wide areas of the Australian Region cannot be of very recent development. There is no evidence of marked discontinuities separating the affinities between species in Malaysia and in northern Australia. Consequently such genera and species must have been in contact at the boundaries of these areas for a long period. Examples of such genera include *Themeda*, *Dichanthium*, and *Bothriochloa* (Gramineae); *Carex* and *Fimbristylis* (Cyperaceae); *Dioscorea* (Dioscoreaceae) which is represented by an outlying species in the South-West Province; *Acacia* and *Albizia* (Leguminosae–Mimoseae); *Dodonaea* (Sapindaceae), and certain members of the Euphorbiaceae, Myrtaceae, and Rutaceae. Furthermore the palaeobotanical evidence in such cases as *Elaeocarpus* (Elaeocarpaceae), *Rhytidocaryon* (Menispermaceae), and *Symplocos* (Symplocaceae) shows that tropical elements were present in southern Australia even in the early Tertiary. For these reasons it seems impossible to accept the view that the comparative lack of obviously "Australian" elements in Malaysia may be due to a recent continental drift resulting in a previously non-existent contact between these floristic regions. Consequently the author is unable to subscribe to the Wegenerian hypothesis as a satisfactory method of explaining certain peculiar plant distributions. It must also be recalled that the geological evidence is not in favour of continental drift.

It is thus necessary to accept the principle of continental stability, at least for the period covering the major evolution of the angiosperms and until a scheme, in better accord with the above facts and with the geological data, can be propounded. If, however, the Australian and Malaysian Regions have had much the same positional relationship to one another over such a long period it is necessary to find an alternative explanation for the apparently differential migration rates into and from the Australian Region. Fortunately a simple one is available, that is the floristic relationships can be understood if ecological factors are deemed to be as important as geographic ones.

Earlier in this study (Part B, Section IV) the view was expressed that during the Pleistocene the climate of northern Australia would have been wetter than at present. Under such circumstances it would have been quite possible for dense communities of tropical species to have existed in the north and north-east of the continent. The natural source for such species, apart from endemic elements, would have been New Guinea during the intermittent land contacts of the Pleistocene. On the other hand the great majority of the Australian elements are light-requiring species which could not have penetrated either into or through such tropical communities. Ecologically, on the basis of present day tolerances, the succession seems to be from an open forest to a monsoon or rain-forest type. With an expansion of such a vegetation barrier into northern Australia migration of the great majority of Australian elements into Malaysia would have been inhibited by the competition factors.

It has also been noted by Holttum (1940) that species adapted to a seasonal type of climate tend to remain vegetative in their growth and fail to initiate flowering under an equable climate. His remarks are based on the behaviour of plants in the Botanic Gardens at Singapore but the inference is that this type of climate can be a very effective migration barrier.

This opinion concerning the effective nature of a dense forest barrier to migration is supported by the remarks of van Steenis (1934*a*, 1934*b*, 1936) regarding the difficulties of accounting for the migration of temperate elements into and through Malaysia. There is also the evidence provided by Webb (1958) that when rain-forests in north-eastern Queensland are destroyed or damaged the primary regrowth, at least, includes phyllodineous *Acacia* spp. and *Eucalyptus* spp. These species are otherwise limited to marginal areas and clearings (Francis 1951). A similar situation is presented in Tasmania where Gilbert (1958) when discussing the establishment of Eucalypts on areas carrying temperate rain-forest writes "no matter how much seed is applied, an intact understorey is an absolute barrier to Eucalypt regeneration". Thus only where the delicate balance within the community is seriously disturbed can light requiring elements of the Australian type become established and their persistence is directly related to the capacity of the denser community to regenerate.

According to certain global classifications of climate, such as those of Köppen (1931) and Thornthwaite (1948), northern Australia and southern New Guinea have closely similar climates. Ecologically this is misleading as the former has a continental and the latter an island climate. There are also great differences in the topography so that in New Guinea well-watered valleys provide, in areas of comparable rainfall, a range of favourable habitats which are quite lacking in northern Australia. In fact only within limits along the eastern coast are rain-forests able to persist at the present time. The distribution of these has been given by Francis (1951) and the relatively small areas in North-East Queensland which carry forest comparable with that widespread in New Guinea has been the subject of comment by Brass (1953). Thus despite the analyses by the climatologists, dense forests of a tropical type are only found, in Australia, where the rainfall is both high and well distributed throughout the year. That is to say it is the occurrence and length of a dry season, quite as much as the quantity of the precipitation, which governs the development of certain vegetation types. If the climatic indices for rainfall efficiency are plotted, according to the method of Prescott and Thomas (1949), for the areas of Cairns as compared with Kokoda and for Darwin as compared with Port Moresby a better idea of the respective growing seasons can be obtained (Fig. 12). From this it may be seen that though the graph for Cairns shows a marked peak, as compared with the prevailingly wet climate at Kokoda, the cool season precipitation is sufficient to maintain growth. When, however, Darwin is compared with Port Moresby it can be seen that the continental area has a dry season of at least six months while at Port Moresby the cool season, though of a comparable period, is not so markedly dry. This may explain why in northern Australia patches of so-called "rain-forest" of a very depauperate type are limited to narrow fringing communities along water courses and rivers whereas at Port Moresby Australian elements are replaced by denser communities wherever locally suitable conditions permit. If the climate of northern Australia was much wetter the fringing communities could become continuous with those of eastern Queensland and, geographical factors permitting, with those of New Guinea. Against such a barrier it would be extremely difficult for Australian elements to extend far into Malaysia.

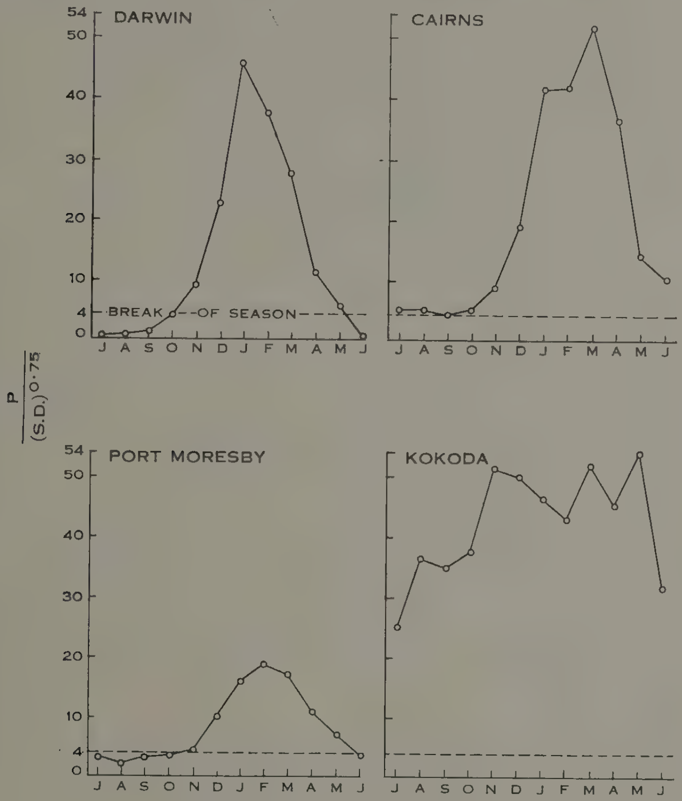

Fig. 12.—Climatic indices.

The strong Malaysian affinities of these fringing communities in northern Australia makes their association with the Pleistocene migration period inevitable. It follows that, though there have been arid phases of considerable or great severity during the post-Pleistocene, conditions have never resulted in their complete elimination. This does not mean that the north has never been more arid than it is at present. Such communities could have been re-established from an even more limited number of refugia during intervening pluvial phases. They do, however, indicate the relative permanence of the Tropical Zone since the Pleistocene. Probably the climatic variations have promoted the selection of biotypes adapted to the more pronounced dry season type of climate though it is not impossible that the original migrants may have included some with this character. The occurrence of a "dry monsoon" type of climate in various areas of Malaysia and the association of "Australian" elements with such areas has been discussed by Airy Shaw (1942). Since this association indicates a marked adaptation of the Australian elements to this type it must have been present over a wider area at some period when migration was possible. This suggests (*a*) that the climate was not consistently pluvial throughout the intermittent Pleistocene contacts with New Guinea, or (*b*) there may have been some gradation in precipitation between the western and eastern parts of the land bridge, or (*c*) that such climatic conditions occurred at an earlier period of land continuity between the Regions. Under (*a*) and (*b*) the effectiveness of the ecological barrier is reduced unless it is postulated that the final stages were the most pluvial and hence there was an elimination of many of the northward moving migrants. An earlier migration might explain occurrences in the Celebes and in New Caledonia and New Zealand and in this case also a later elimination of Australian types would have occurred.

As a final point it should be recalled that the recognition of an "Australian" or a "Malaysian" element is not a simple process. Some cases may appear to be obvious, as in *Banksia* and *Eucalyptus*, but, without a critical analysis and also cytotaxonomic data, it must be impossible to say with any real confidence whether a particular taxon originated in or migrated through or from one region rather than the other. Until more accurate data are available speculation must suffer from being based on fragmentary evidence.

There is also evidence that climatic barriers, as opposed to those formed by geographical separation, has affected the distribution of fauna in the Malaysia–Australia area. Mayr (1953), for example, states that the separation between Australia and New Guinea has been strengthened by the aridity of the former area. Tate (1953) in discussing mammalian distribution in the Cape York Peninsula indicates that open forest conditions have permitted Australian species to push northwards into New Guinea but southward expansion of forest species from New Guinea has been inhibited by the interruption of the rain-forest south of the North-East Queensland area.

Other comparisons with faunal distributions are on a broader basis. Thus Myers (1953) suggests that the fact that there are no freshwater fishes native to New Zealand is evidence that there has been no direct communication with either Australia or South America. Gressitt (1956) in a paper on distributional patterns in Pacific Island faunae provides a series of maps which show distinct similarities to those of certain plants. There is, for example, some evidence concerning movement along van Steenis's Luzon and New Guinea tracks. There is also evidence of the Malaysian character of the representatives in North-East Queensland similar to that found in plants.

Mayr (1940) in discussing the birds of New Caledonia states that among the older endemics the Papuan influence is strong. It is among the more recent endemics that the Australian influence increases. The Papuan influence is reported as being still stronger in the New Hebrides. He suggests that the lack of New Zealand elements may be due to climatic factors, a remark that is not in complete accordance with his comments concerning distribution in Malaysia (Mayr 1953). It is possible that this apparent discrepancy is due to the differences between types of tropical climate and between tropical and temperate climates.

Solem (1958) in a study of the biogeography of the New Hebrides states that land snails in that area show a relationship with those of New Zealand. He also states that the geological evidence does not indicate a former land continuity with New Caledonia. According to this author the land snails in the southern hemisphere represent an ancient migration (Palaeozoic) from the northern hemisphere, the primitive types being preserved in southern refugia. Both Australia and New Zealand are considered to have received their complements from New Guinea and it is possible that the New Hebrides had a longer connection with New Guinea than had New Caledonia. Australia received several waves of migrants, the latest being referred to the late Tertiary—the palaeo-Oriental fauna in eastern Queensland.

In this paper an attempt has been made to treat Australian plant geography in terms of broad concepts and general trends. It has not been possible to examine all the zoological data with which the botanical information should be correlated but the above references may be sufficient to show that there is a similarity between the problems concerning faunal and floral distribution in the areas of Malaysia, the Australian Region, and the South-West Pacific. Despite the longer time range taken into account by the zoologists there is evidence that there are similar trends. It is clear, for example, that representation in New Caledonia, like that in the North-East Queensland area, may be closely related to climatic changes as well as to geographical ones.

To sum up, the flora of the Australian Region includes elements which suggest Antarctic, tropical, and northern hemisphere origins as well as autochthonous elements. The latter have developed from a pre- or early Cretaceous flora of an unknown type, from the invading elements, or have arisen within the Region as a result of the interaction between these originally alien elements. What angiosperms the earliest flora may have included is not known. Medwell (1954) has described two angiosperm leaves from lower Cretaceous beds in Victoria but the report of Glaessner and Rao (1955) concerning beds of a similar age in the north-eastern Flinders Range, in South Australia, lists only cycads and conifers among the seed plants.

There have been several periods of active migration which are indicated by the geological history as well as by phytogeographic data. The most important migrations which must, at least to some extent, have been in both directions seem to have occurred in the pre-Tertiary, the early to mid Tertiary when the continent included a New Guinea composed of its present southern section, and, finally, a third period during the Pleistocene when there was periodic reunion with a New Guinea which now included its central and northern areas. During the middle period interchange was possible with eastern Malaysia and possibly also with New Caledonia and New Zealand (or with land areas in these parts of the Pacific) via the New Guinea track of van Steenis. Comparable relationships may be deduced from the data given by Skottsberg for the Hawaiian flora (1940). Contact with these Pacific areas had ceased by the time of the third principal migration period.

Tasmania was connected with the mainland during most, if not all, of the Tertiary and had interrupted communication with it during the Pleistocene. What connections there may have been with Antarctica are still purely speculative but until the Pleistocene there was no geographic barrier to migration to or from the mainland. Such migration and interchange would not have been seriously interrupted by climatic oscillations, though it seems probable that much of the flora of the island, especially at higher elevations, may have been depleted during the period of glaciation. This geographic relationship with the mainland and the climatic effects have resulted in a flora within which the Australian elements are closely related to those on the mainland, and the endemics are mostly adapted to cold habitats. Some of these cold climate elements may represent later migrants from the south but since a number are to be found in the Australian Alps they must include Pleistocene if not pre-Pleistocene elements.

The generic relationships and affinities between Tasmania, south-eastern Australia, New Zealand, and South America pose a phytogeographic enigma. Since one cannot doubt the congenericity, and in some cases the conspecificity, one must accept some continuity of land surfaces and of climatic belts in the past. Acceptance of the Wegenerian hypothesis is made difficult owing to the distance between Australia and South America in the hypothetical Pangaea and also because of the long-standing affinities between the flora of the Australian Region and that of the lands to the north. The idea of land bridges is also difficult to accept.

In contrast to Tasmania the flora of the South-West Province has been isolated by both geographic and climatic factors. It is far from any well-marked migration route and the lack of special affinities with the flora of South Africa is contrary to what might have been anticipated under the drift hypothesis. Communication with either the Tropical Zone or other parts of the Temperate Zone in the east has been possible at various times when the climate was favourable but the great geographic distance and the fact that many of the elements would have been diffusing from the eastern migration route has resulted in a highly endemic flora and the persistence of many relicts. At the generic level many of the taxa have western and eastern groups of species and these indicate a period when the flora of southern Australia may have been virtually continuous, in a floristic sense, and there was free interchange. Such a state of affairs occurred in the early Tertiary but the number of Australian elements which now exhibit this type of distribution shows that continuity persisted until, or re-occurred at, recent periods also.

Interchange with either New Zealand or South Africa must have been limited throughout the Cretaceous and Tertiary but some communication with South America is strongly indicated by the marked generic affinities. Skottsberg (1953) suggests that the ancient flora of the Antarctic continent was of two types, montane and lowland, and that these have progressed into lower latitudes to a different extent. These types have not been recognized here but if Skottsberg is correct then it is possible that most of the Antarctic elements on the Australian continent belonged to the lowland type. Montane elements may be represented by some of the Tasmanian mountain plants which also occur in New Zealand.

The picture formed by consideration of migrations in relation to the flora of the Australian Region is that the route along the ranges and coasts of eastern Australia has been extremely important and that the route is of great antiquity. This means that North-East Queensland and Tasmania are the most important "portals" to the Region. In each of these areas there are elements which have either failed to penetrate further or have not yet had time to disseminate. Within the Region as a whole migration has involved a sorting-out of the elements according to climatic tolerances and adaptability, i.e. a latitudinal effect as compared to the longitudinal one on the main route. This latitudinal and climatic selection of the material available has been modified by the size of the continental area. Within this area some gradation of rainfall must always have been present and this gradation would have been concentric in nature. Thus the vegetation has been affected by (1) north and south migration related to climatic variations and the adaptability of the taxa; (2) west and east movements due to migration within climatic zones; and (3) inward and outward movements of ecological zones due to climatic changes which particularly involved increases and decreases of rainfall, as opposed to temperature effects which must have played an important role under (1).

It is not to be expected that a discussion of this nature will result in final conclusions. Many more data are required concerning affinities between taxa within the Region and between taxa also present in other regions. We also require more detailed information about distribution patterns. Nevertheless, despite the inadequacy of some of the data, knowledge is sufficient to justify the sketching of the broader features. Incomplete and imperfect as the resulting picture may be it is profitable to view it as a whole and so avoid errors due to overconcentration on localized details. It is hoped that the data presented here will serve this purpose and that the opinions expressed will contribute to the clarification of the many problems posed by plant distribution and taxonomic relationships in the southern hemisphere.

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FLORAL HISTOGENESIS IN THE MONOCOTYLEDONS

IV. THE LILIACEAE

By C. Barnard*

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Summary

An account is presented of floral histogenesis in *Bulbine bulbosa* R.Br. and *Stypandra glauca* R.Br.

The apex of the floral axis in both species has a two-layered tunica, and bracts arise through the periclinal division of cells of the inner layer of the tunica (hypodermis). In *Bulbine*, axillary flower primordia are initiated in the periclinal division of subhypodermal cells; in *Stypandra* the flower primordia are terminal and arise directly from the apices of branches of the inflorescence.

In both species the perianth members originate, in the same manner as the bracts, through periclinal divisions in cells of the hypodermis. Periclinal divisions may occur in the cells of the outer tunica layer (dermatogen) after the primordia are well formed. Divisions in subhypodermal cells in the area of perianth initiation are associated with the formation of a provascular strand and it is doubtful if such divisions contribute anything to the tissue of the perianth primordium itself. The stamens are initiated in the periclinal division of both hypodermal and subhypodermal cells.

In *Bulbine* the carpels develop through periclinal divisions in the hypodermis and dermatogen. The placentas appear to arise through divisions in subhypodermal cells as structures adnate to the carpels. In *Stypandra* the carpels arise in a quite different manner through the periclinal division of subhypodermal cells. The margins of the carpels develop as the placentas and there is no suggestion in the early ontogeny of the gynaecium that the placentas have an independent origin.

I. Introduction

Very few studies have been made of the histology of floral organogenesis in the monocotyledons. Published descriptions of such studies are found in the present series of papers (Barnard 1955, 1957*a*, 1957*b*, 1958), which have given examples from the Gramineae, the Juncaceae, and the Cyperaceae; in a paper by Holt (1954), which dealt with members of the Gramineae; in a paper by Kaussmann (1941), which deals *inter alia* with *Aloe eru*; and in an article on *Tulipa* by Sass (1944). Barnard (loc. cit.) concludes that the mode of origin of the various floral structures indicates that bracts, glumes, and perianth members, together with the carpels, are to be interpreted as appendages which are foliar in nature and homologous with leaves, whilst the stamens and flower primordia are cauline in nature. The flower is thus interpreted as a reduced branch system, the perianth and carpels as foliar structures on its main axis, and the stamens as reduced branches bearing microsporangia. Sass (1944) and Kaussmann (1941), on the other hand, found that the stamens as well as the perianth arose in the same fashion as vegetative leaf primordia.

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Few studies have been made of floral histogenesis in dicotyledonous flowers, and, on the whole, these studies have supported the classical concept of the nature of the flower, i.e. all parts, including the stamens, are to be regarded as appendages homologous with leaves.

In the present communication, the histology of floral organogenesis is described in two species belonging to the family Liliaceae: *Bulbine bulbosa* R.Br. and *Stypandra glauca* R.Br. *Bulbine* belongs to a very large tribe, the Asphodeleae, which seems to represent the main stock of the family (Hutchinson 1934): *Stypandra* belongs to a comparatively small tribe, the Dianelleae. Payer (1857) described and illustrated floral organogenesis in four genera of the Liliaceae, viz. *Aloe atrovirens*, *Lilium candidum*, *Lomandra longifolia*, and *Charlwoodia congesta*. Since then a number of authors have confirmed Payer's general picture of floral ontogeny in this family by studies of development in other genera (e.g. Jones and Emsweller 1936; Sass 1944). The only reports on the histogenesis of floral development are descriptions for *Tulipa* (Sass 1944) and *Aloe* (Kaussmann 1941).

II. MATERIALS AND METHODS

Species of *Bulbine* L. occurring in Australia have been placed under *Bulbinopsis* Borzi by Kraus in the second edition of "Die Natürlichen Pflanzenfamilien" of Engler and Prantl. In the present paper Australian usage is followed and the species retained under the name *Bulbine*. *Bulbine bulbosa* R.Br. bears yellow flowers in a terminal bracteate raceme on a leafless stem and the pedicels are articulate close to the flowers. Developing racemes were collected from naturally occurring plants in the fields at Canberra, during the latter part of July and early August. They were fixed in formalin-acetic-alcohol; serial longitudinal and transverse sections were made in paraffin wax at 7 μ; and staining was done in iron alum haematoxylin and erythrosin. Drawings were made by photographing the section and tracing a projected enlarged image of the negative. Additional clarity in detail was sometimes obtained by reference to adjacent sections of the series.

Material of the developing inflorescence of *Stypandra glauca* was also collected from naturally occurring plants at Canberra during July. Procedures were similar to those used for *Bulbine*.

III. BULBINE BULBOSA R.Br.

(a) *Morphology*

The developing raceme of *Bulbine* is shown in Plate 1. All except the three youngest bracts have been removed, thus disclosing the apical dome of the inflorescence axis and flower primordia in various stages of growth and differentiation. The spiral arrangement of the bracts upon the axis is shown in Figure 1. The first and second perianth members form in lateral positions upon the flower primordium; the third perianth member occupies an anterior and the fourth a posterior position. The three stamens of the outer whorl arise in the axils of the three outer perianth members, and the three stamens of the inner whorl arise in the axils of the three inner perianth members. The stamen primordia are well developed before the carpel primordia arise. The carpel primordia appear as three crescentic ridges which arise on the flattened apex of the flower primordium and alternate to the three inner stamens. The three ridges become confluent and the placentas develop at their junctions (Plate 1, *pl*).

(*b*) *Histogenesis*

The cells of the apex of the axis of the inflorescence are organized into a two-layered tunica and a corpus (Figs. 2–6). The outer layer of the tunica or the dermatogen is always very distinct because of the regular rectangular shape of its cells and their orientation as a single layer. Cells of the dermatogen divide only by anticlinal walls. The inner tunica layer or hypodermis also is usually quite well defined by the size and regular arrangement of its cells. The cells of the hypodermis are generally larger than those of the dermatogen and outer layers of the corpus, and tend to be longer radially than they are tangentially. Division of cells of the hypodermis is only by anticlinal walls except where a bract or flower primordium is being initiated. The first divisions initiating a bract occur at a little distance (100 μ) back from the apex of the dome (*vide* Figs. 2 and 3, *br*). There is therefore only a short apical dome in which the hypodermis occurs as a single layer. The cells of the corpus

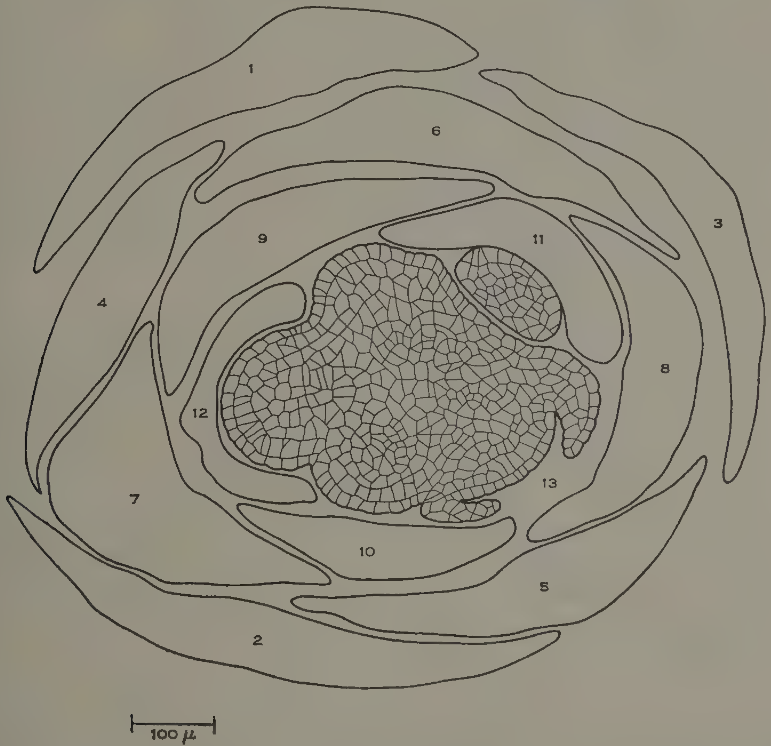
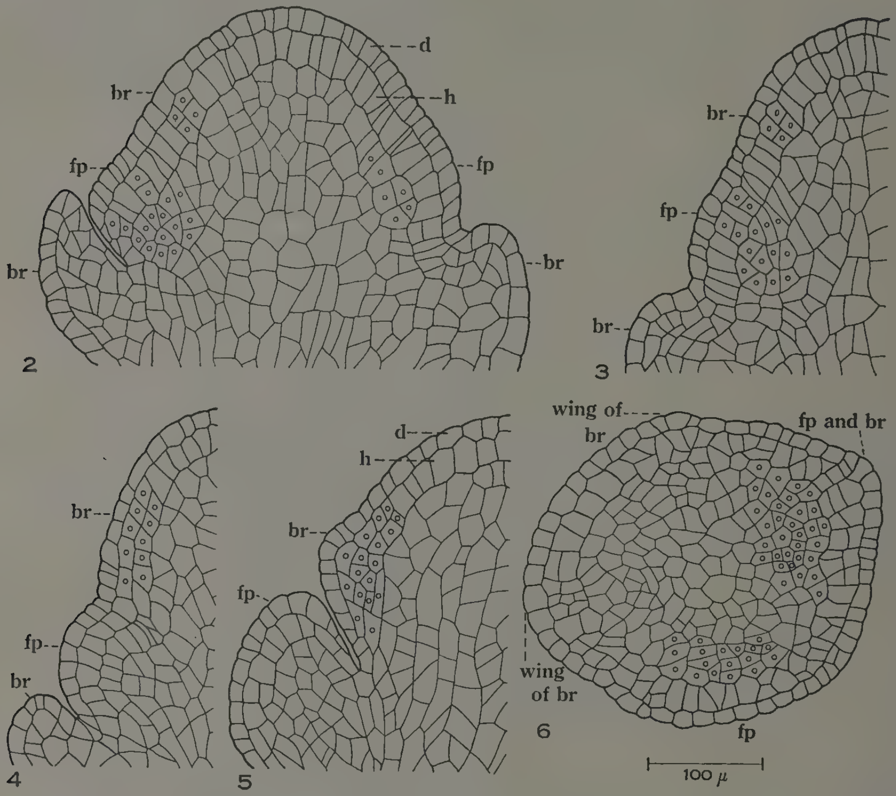


Fig. 1.—*Bulbine bulbosa.* Transverse section through tip of raceme, showing arrangement of bracts. Oldest 1, youngest 13. Flower primordia are seen in the axils of bracts 11 and 12.

above the point of initiation of the youngest bract contain dense cytoplasm and stain deeply like cells of the dermatogen and hypodermis in this region. Divisions at the tip of the corpus appear to take place in different planes at random but back from the tip the cells become orientated in files. Back from the tip of the corpus the cells also become vacuolated and stain less densely.



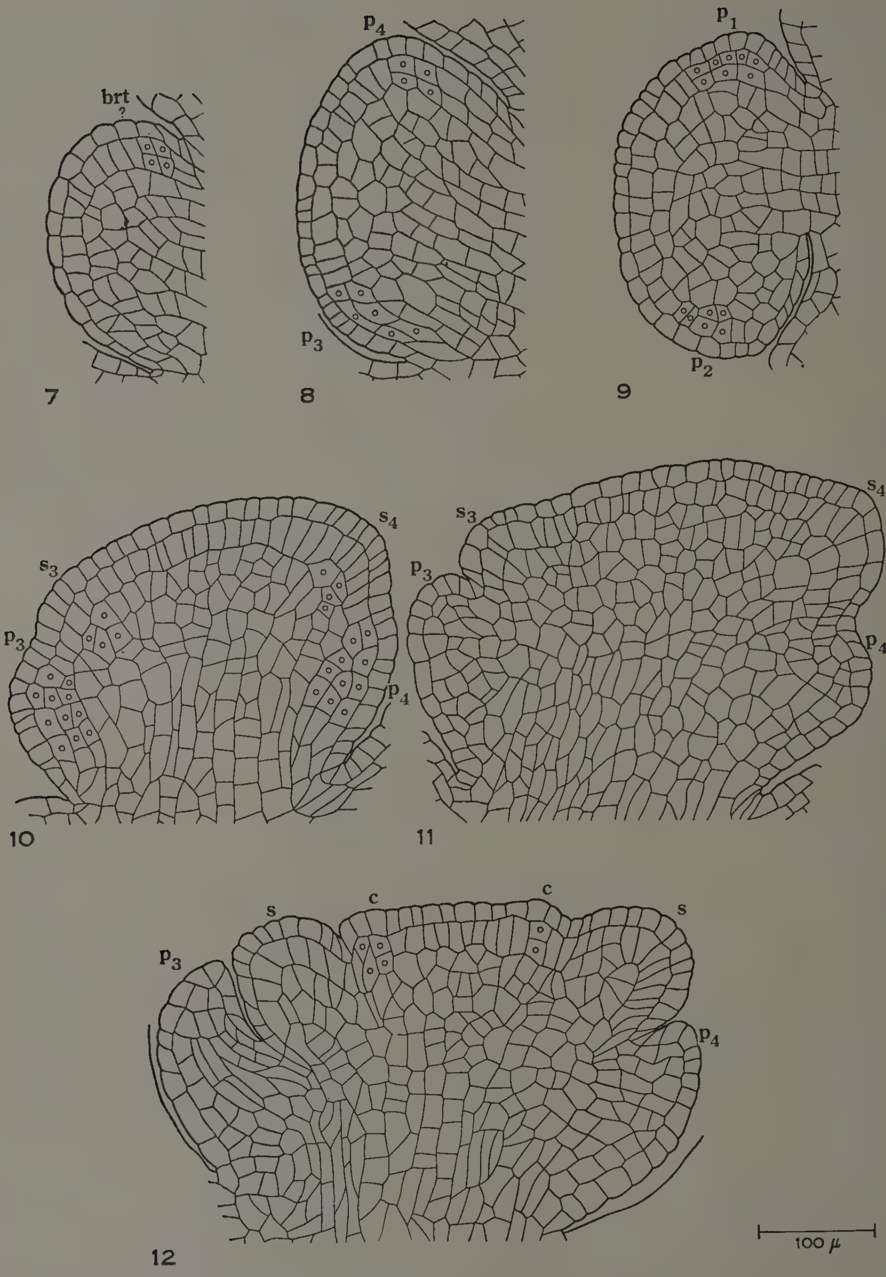
Figs. 2–6.—*Bulbine bulbosa.* Figs. 2–5, median longitudinal sections through the apex of the axis of the inflorescence. Fig. 6, a transverse section through the apex of the axis of the inflorescence, showing organization of tissues of the apex and origin of bracts and flower primordia. *d*, Dermatogen; *h*, hypodermis; *br*, bract; *fp*, flower primordium. The cells particularly concerned with the origin of the bracts and flower primordia are indicated by small circles.

Bracts arise by the periclinal division of hypodermal cells and the continued anticlinal division of the dermatogen cells. The first sign of the initiation of a bract is the periclinal division of several hypodermal cells (Figs. 2 and 3, *br*). The area in which these divisions occur extends transversely about one-third of the way around the circumference of the axis. Hypodermal cells above and below also divide periclinally until a crescentic shaped ridge is formed which involves six or seven cells in the vertical direction (Figs. 4 and 5, *br*). Continued division by periclinal and inclined walls of the derivatives of the original hypodermal cells results in the further growth of the young bract primordium (Fig. 5, *br*). Cells of the outer layers of the corpus near the centre of the area of bract differentiation become vertically elongate and may divide by periclinal walls. These cells, however, do not contribute to the growth of the bract primordium; they differentiate as part of the provascular strand in the axis which later becomes continuous with the provascular strand of the bract.

The flower primordia arise in the axils of the bracts as the result of the division of cells of the outer layers of the corpus and the hypodermis. Usually four cells in a vertical plane are concerned in the corpus. The centrally placed cells divide by periclinal walls and the upper and lower ones of the vertical tier by inclined walls (Figs. 2 and 3, *fp*). Further division of these cells in the same planes gives rise to a slight bulge on the surface of the axis (Figs. 2–4, 6). Several hypodermal cells also usually divide by periclinal or inclined walls (Figs. 2, 3). The outer of these becomes a hypodermal cell in the young flower primordium; the inner one part of its corpus. Cells of the dermatogen continue to divide only by anticlinal walls and so it remains a single discrete layer.

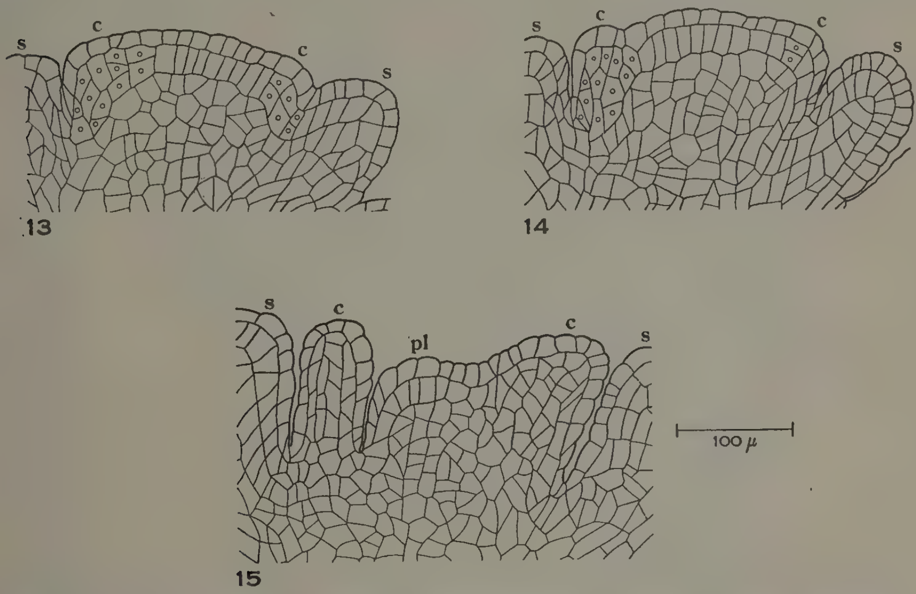
In the young flower primordium the dermatogen and hypodermis are recognizable as discrete layers surrounding the corpus (Fig. 7). The origin of the perianth members is seen in the periclinal division of cells of the hypodermis. In radial longitudinal sections through the raceme and median through the flower primordium the origin of the third and fourth perianth members is observed (Fig. 8), whilst in transverse sections the origin of the first and second perianth members is visible (Fig. 9). In longitudinal sections through very small flower primordia periclinal divisions are frequently observed in several hypodermal cells on the posterior or adaxial side of the primordium, and these divisions (Fig. 7, *brt*?) do not seem to be associated with the origin of the fourth perianth segment. They occur too early and are situated too low on the flower primordium to be interpreted as the first divisions in the differentiation of the fourth perianth member. It is possible that they represent a vestigial bracteole. Growth of the young perianth members is by the continued division of derivatives of the original hypodermal cells (Figs. 10, 11). Meristematic activity then becomes concentrated at the tip and margins of the perianth members, and periclinal divisions may occur in dermatogen cells (Fig. 12). As growth continues, the centre of meristematic activity shifts until it is located at the base of each of the perianth units. The fourth perianth segment during its early development is clearly distinguishable from the third member, not only by its position on the flower primordium but also because of its different shape. The primordium of the fourth perianth segment is broad and has a flattened or almost dome-shaped apex in section which contrasts with the slender pointed primordium of the third perianth member. The stamen primordium arises primarily as a result of the division of subhypodermal cells. In the areas of stamen differentiation, hypodermal cells elongate radially, and then periclinal and inclined divisions occur in subhypodermal cells (Fig. 10). Periclinal divisions may also take place in the elongated hypodermal cells; and when this occurs the outer of the two cells resulting from the division divides only anticlinally, so that the continuity of the hypodermis is quickly re-established.

Following the initiation of the stamens a number of divisions occur in the cells of the corpus and the apex of the flower primordium becomes broader and flatter.


brt
?
7
p4
p3
8
p1
p2
9
s4
s3
p3
p4
10
s3
s4
p3
p4
11
c
c
s
s
p3
p4
12
100 μ

Figs. 7–12.—*Bulbine bulbosa.* Sections illustrating the development of the flower primordium and the origin of perianth segments, stamens, and the carpellary ridge. Figs. 7, 8, and 10–12 are median radial longitudinal sections through the flower primordium, whilst Fig. 9 is of a flower primordium cut transversely, i.e. at right angles to the plane of the axis of the inflorescence. p_1–p_4, perianth members; s, s_3, s_4, stamens; c, carpellary ridge; *brt?*, possible vestigial bracteole.

The first indication of the formation of the carpellary ridge is the periclinal division of hypodermal cells (Fig. 12). These divisions result in the formation of three small crescentic ridges around the edges of the flattened growing point of the flower primordium (*vide* Plate 1, flower in which perianth members are labelled). Immediately following the periclinal division of the hypodermal cells, periclinal divisions occur in cells of the subhypodermis or outer cells of the corpus (Fig. 14). These divisions in the deeper tissues raise the level of the whole growing point of the flower primordium. The carpellary ridges grow into the carpel walls by the continued division of derivatives of the original hypodermal cells, and the three placentas seem to arise primarily as a result of the divisions in the subhypodermal cells (Fig. 15). The intimate association between the placental tissue and the tissue of the carpel wall makes it difficult to be certain on this point. In further growth of the carpel walls, divisions of "apical" hypodermal cells are prominent and periclinal divisions occur in dermatogen cells. Periclinal divisions in dermatogen cells are also observed near the tips of the placentas.



Figs. 13–15.—*Bulbine bulbosa.* Median longitudinal sections of portion of flower primordium, showing origin of carpels (*c*) and placenta (*pl*).

IV. Stypandra glauca R.Br.

(*a*) *Morphology*

The flowers of *Stypandra glauca* are borne in a short loose terminal cymose panicle. The branches of the inflorescence arise distichously and each is subtended by a bract; this bract is large and like a foliage leaf for the lower branches, but becomes progressively smaller for distal branches. The branches twist during their development so that when mature the distichous nature of their arrangement is not clearly apparent. The flowers are borne in twos and occasionally threes (Plate 2) on slender pedicels. A branch of the inflorescence divides pseudo-dichotomously, for the two resultant apices are at first almost equal in size and similar in appearance (Fig. 16). The apex, which represents the lateral branch of this division, is recognized by its position relative to previous branches. The apex of the branch differentiates as a flower primordium (Fig. 17). The apex of the lateral may also differentiate directly as a flower primordium—which results in a pair of flowers—or it may again divide. If it divides, each of the new apices differentiates as a flower, and a group of three flowers is formed.

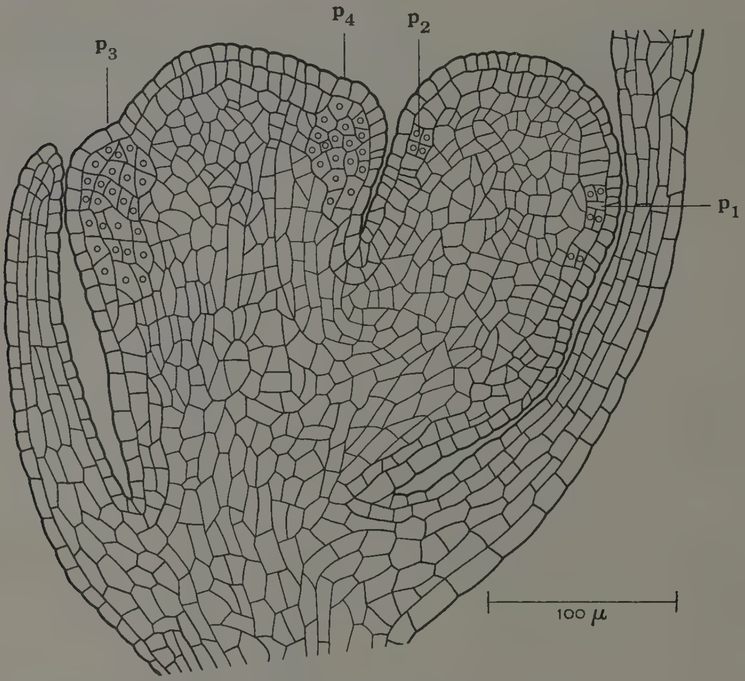


Fig. 16.—*Stypandra glauca.* Median longitudinal section through two young flower primordia in which the perianth (p_1–p_4) is differentiating. The flower primordia represent the apices of two branches of the inflorescence which have developed from a pseudo-dichotomous division.

The formation of the perianth segments and stamens upon the flower primordia (Plate 2) is as in *Bulbine.* The three carpels, however, arise clearly as separate structures. Each appears as a V-shaped ridge upon the flattened apex of the flower primordium. The point of the V grows more rapidly than the sides, so that shortly it develops as a cone with a cleft down one side. As growth continues the three carpels become closely pressed one against the other and coalesce; the ovary becomes trilocular and ovules are borne on axile placentas. The tips of the three carpels fuse and the style develops from the fused tip.

(*b*) *Histogenesis*

The apex of a branch of the inflorescence has a two-layered tunica, but the distinction between the tunica and corpus is not very clear. This is because the cells of the outer layers of the corpus tend to be regularly arranged like those of the dermatogen and hypodermis. The bracts arise through periclinal divisions in the hypodermis in the same way as in *Bulbine*. Periclinal division of subhypodermal cells in the area of bract differentiation is associated with the formation of the provascular trace. These divisions do not contribute to the tissue of the bract primordium. The provascular strand leading to the bract is clearly discernible at the time when the first divisions initiating the bract are occurring.

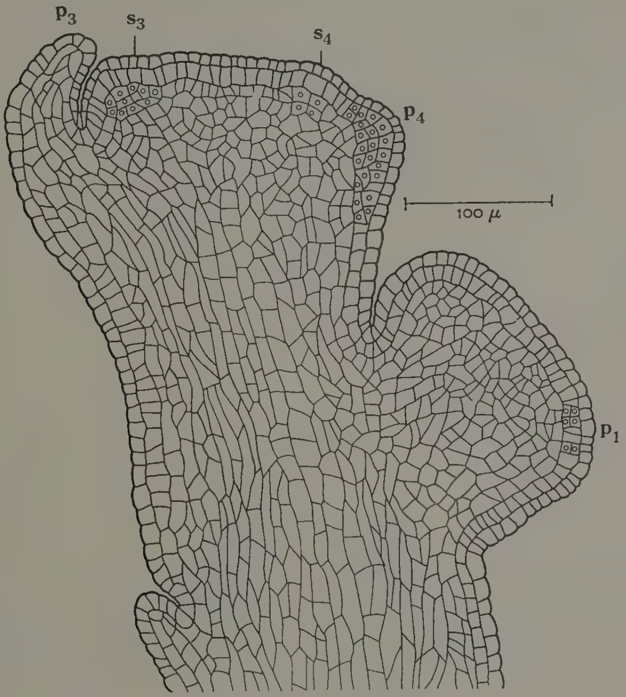
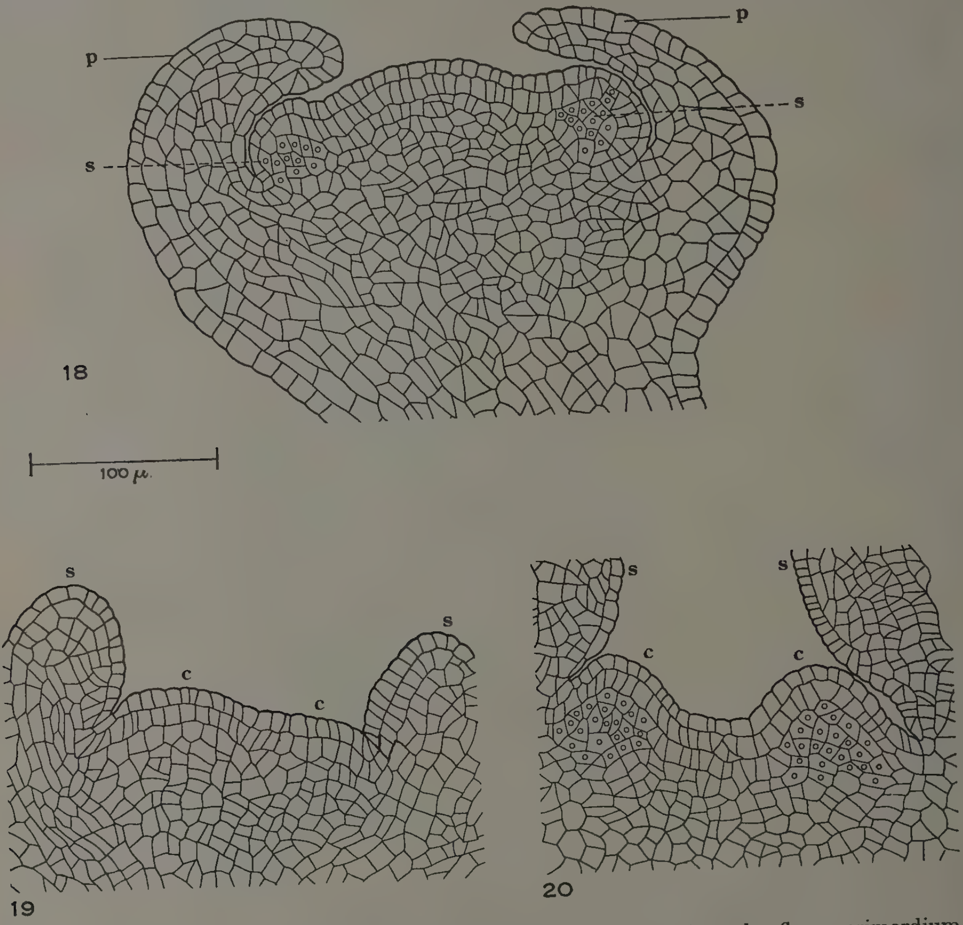


Fig. 17.—*Stypandra glauca*. Median longitudinal section through two young flower primordia as in Fig. 16. One primordium is more advanced than the other and shows the origin of two stamens (s_3, s_4). In the other, periclinal divisions in the hypodermis probably represent the origin of the first perianth member (p_1).

The flower primordia are terminal and arise directly from the apices of the branches (Fig. 16). The dome of the branch apex becomes slightly flatter and the perianth members are initiated in periclinal divisions in the hypodermis and subhypodermis (Figs. 16, 17). The periclinal divisions in the subhypodermis are associated with the formation of the provascular strand and often seem to precede the divisions in the hypodermis. Thus a clearly defined provascular strand may be present leading to the place where a perianth member will subsequently be formed. Whilst derivatives from the hypodermal cells contribute the bulk of the tissue of the perianth member, derivatives from subhypodermal cells may also be concerned.

The dome of the flower primordium becomes flatter preceding the initiation of the stamen. The stamen primordia arise by the periclinal division of subhypodermal cells and hypodermal cells (Figs. 17, 18) in the same manner as in *Bulbine*. Periclinal division of hypodermal cells is not very common and the bulk of the growth of a stamen primordium is the result of subhypodermal activity. Dermatogen cells continue to divide only by anticlinal walls.



Figs. 18–20.—*Stypandra glauca*. Fig. 18, median longitudinal section through a flower primordium, showing the origin of the stamens (*s*) in periclinal divisions mainly in subhypodermal cells. Figs. 19 and 20 are longitudinal sections of the centre of the flower primordium, showing the origin of the carpels through divisions in subhypodermal cells. Periclinal divisions do not occur in either the dermatogen or hypodermis.

The carpels arise by the periclinal division of subhypodermal cells (Figs. 19, 20). Periclinal divisions never occur in the dermatogen and rarely in the hypodermis.

The initiation and early growth of the carpel primordia are due almost entirely to divisions in the subhypodermis. This manner of carpel origin is quite different from that in *Bulbine* and from any other species described in the present series of papers.

V. Discussion

The organization of the apex of the axis of the inflorescence in *Bulbine* and *Stypandra* into a two-layered tunica and a corpus is similar to that in the other monocotyledons described in the preceding papers of this series. The distinctness of the inner layer of the tunica is not always very marked, but periclinal divisions occur in this layer only where new organs are being initiated. Eckardt (1941) says that the vegetative apices of *Liriope muscari* (Dcne) Bailey, and *Mondo japononicum* (L.fil.) Farwell, which belong to the family Liliaceae, seem to have two-layered tunicas and his illustrations support this view. Rüdiger (1939) records a two-layered tunica in the vegetative growing point of *Aloe* (Liliaceae). Stant (1952) interprets the apex of *Convallaria majalis* (Liliaceae) as having a tunica of one layer, but her drawing seems to show that the tunica is of two layers and periclinal divisions in the second tunica layer occur at the point of origin of a leaf. The presence of a two-layered tunica in the floral axes of *Bulbine* and *Stypandra* is in conformity with other genera examined in this family. The two-layered tunica seems to be a very common feature of both the vegetative and the floral axes in monocotyledons.

The pattern of floral histogenesis in *Bulbine* and *Stypandra* differs in several important respects from that of the Juncaceae, Cyperaceae, and Gramineae; and the mode of origin of the carpels in *Stypandra* is entirely different. The foliar type organs, i.e. the bracts and perianth members, in *Bulbine* and *Stypandra* arise as a result of periclinal divisions in the hypodermis. In *Stypandra*, division of cells in the subhypodermis may also make some contribution to the tissue of the young perianth segment primordium. Cells of the dermatogen continue to divide only by anticlinal walls. In the Gramineae and Cyperaceae, on the other hand, foliar type organs (glumes, lemma, palea, and perianth units) are initiated by periclinal divisions in the dermatogen as well as in the hypodermis, and derivatives of the dermatogen cells contribute largely to the tissue of the new organ. In the Juncaceae these organs have their origin in periclinal divisions in the hypodermis. Periclinal division in dermatogen cells does not take place at initiation but occurs after a small primordium has been formed. Periclinal divisions in dermatogen cells then contribute largely to the apical and marginal growth of the new structure.

The axillary flower primordia of *Bulbine* and the stamen primordia of both *Bulbine* and *Stypandra* originate as cauline structures in the same manner as in the previously examined families. These organs are initiated in periclinal divisions in the subhypodermis. Periclinal divisions occur in the hypodermis during differentiation but the periclinal division of subhypodermal cells is mainly responsible for the growth of the young organ. This pattern of histogenesis is different from that of the foliar type organs. Sass (1944) on the other hand concluded that, in *Tulipa*, the primordia of leaves, perianth members, and stamens arose in the same manner. He states that these structures are initiated in the first layer of the corpus and enlarge by cell divisions in the corpus. Sass interprets the apex of the floral axis in *Tulipa* as having a tunica of one layer up to the time of stamen formation. The leaf primordia and perianth primordia arise in the second layer of cells and therefore in the same way as described here for *Bulbine* and *Stypandra*. Lack of adequate illustration of the formation of the stamen in Sass's paper does not permit comment on his interpretation of the origin of this structure. Kaussmann (1941) states that the perianth and stamens in *Aloe* arise in the same way, i.e. by periclinal division of cells in the second layer. His illustration of the origin of the perianth supports the view that it arises by the periclinal division of the second layer; his illustration of the origin of the stamen is not so convincing.

The carpellary ridge in *Bulbine* arises by the periclinal division of hypodermal cells; the periclinal division of dermatogen cells is not involved. In the Gramineae and Cyperaceae periclinal divisions always occur in the dermatogen in carpel initiation, and the early growth of the carpels is largely apical and through the division of dermatogen cells. In *Luzula* (Juncaceae) the carpellary ridge is initiated by periclinal divisions in the hypodermis followed immediately by similar divisions in the dermatogen. Early growth in both the carpellary ridge and the carpel tips is mainly the result of divisions of derivatives of the dermatogen cells. The development of the carpels in *Bulbine* is different, in that periclinal divisions in the dermatogen do not occur at their initiation. The placentas in *Bulbine* seem to arise differently from the carpellary ridge and by the periclinal division of subhypodermal cells. The mode of origin of the placentas and the relation of the placentas to the initiation of the carpellary ridge are the same in *Bulbine* as in *Juncus*. The question of the interpretation of the placentas has been previously discussed in connexion with *Juncus* (Barnard 1958). The present study of *Bulbine* tends to support the view that the placentas are axial or cauline structures fused to the encircling carpellary tissue.

The mode of origin of the carpels in *Stypandra* is quite different from that observed in any of the species so far examined. The carpels in *Stypandra* arise by the periclinal division of subhypodermal cells; rarely, if at all, is there any periclinal division of hypodermal cells; and no divisions of this kind were observed in dermatogen cells. This is in striking contrast to the situation in the Gramineae, the Cyperaceae, and the Juncaceae. In all of these the carpels arise by the periclinal division of both hypodermal and dermatogen cells, and the bulk of the carpellary tissue is derived from the dermatogen of the flower primordium. In *Stypandra* the axile placentas develop from the swollen and fused edges of the carpels and there is no suggestion during early development that the placentas have a separate axial origin. It is clear that the histogenesis of the gynaecium must be examined in many more genera before generalization with respect to the family as a whole can be made.

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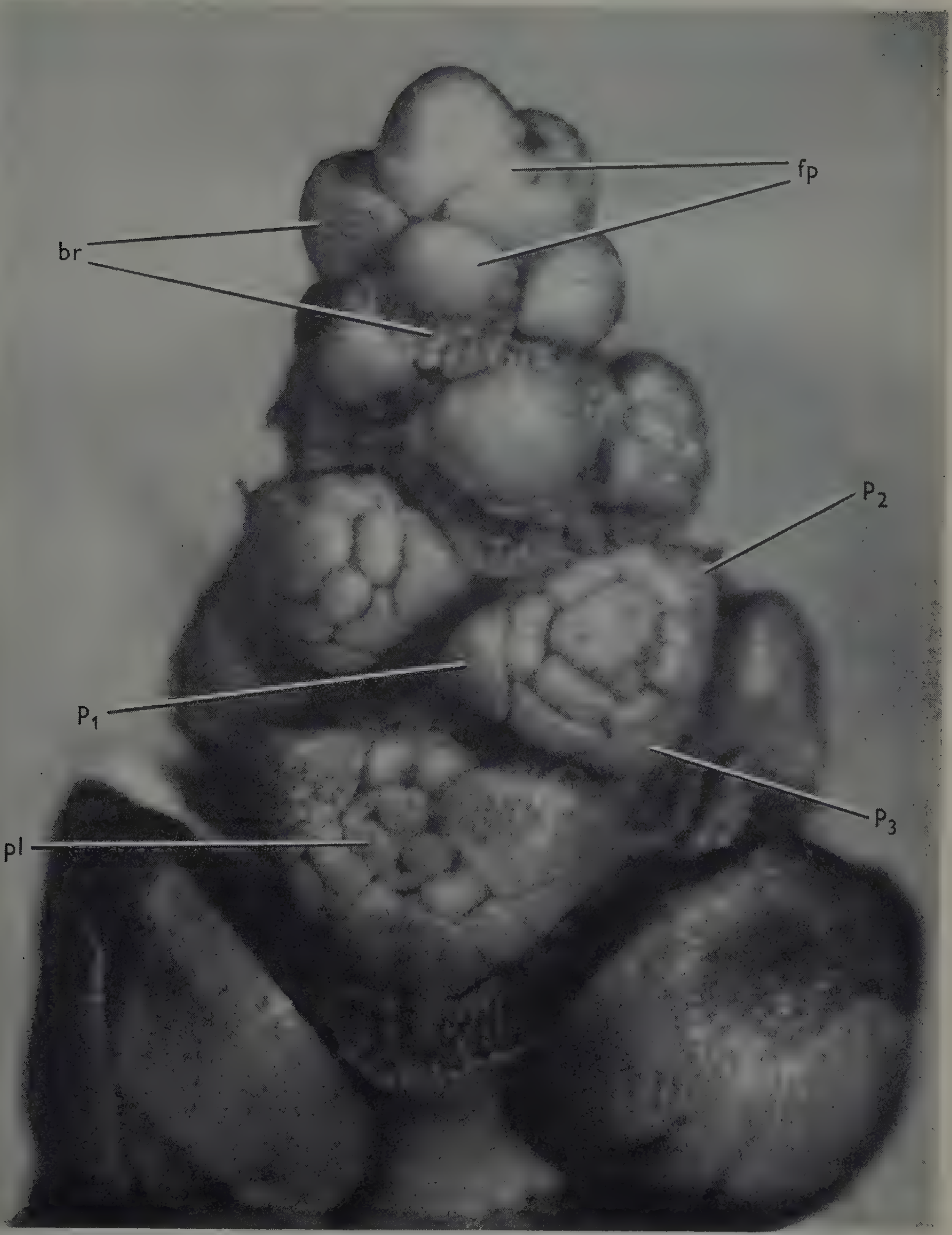
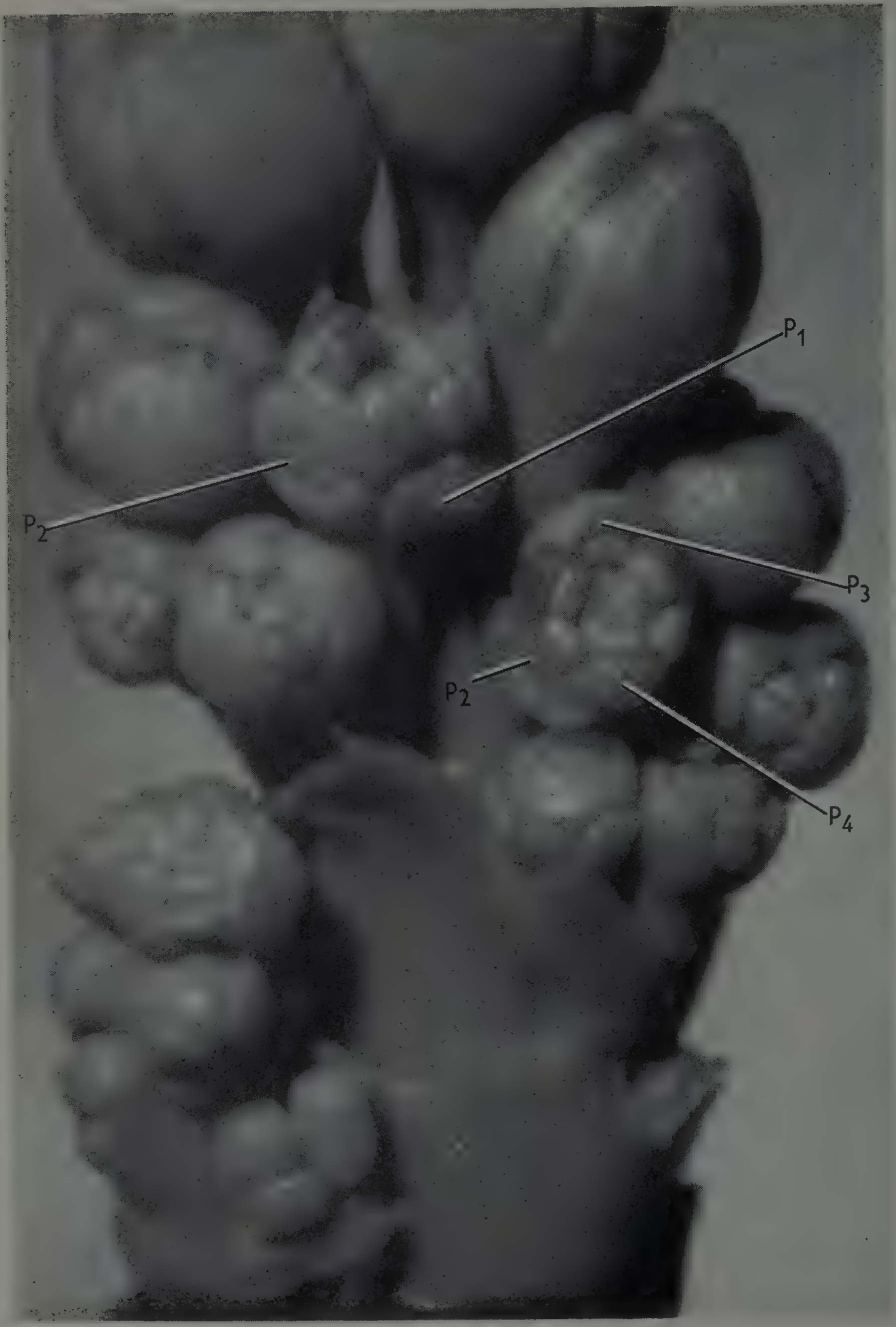


Bulbine bulbosa. Young raceme from which all but the three youngest bracts (*br*) have been removed. Flower primordia (*fp*) are in various stages of differentiation. p_1–p_3, Perianth members; *pl*, placenta. ×69.



Stypandra glauca. Portion of young inflorescence, showing flower primordia in various stages of differentiation. Bracts have been removed and perianth members (p_1 and p_2) broken off to disclose the other parts of the flower. ×74.

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ANATOMICAL AND MORPHOLOGICAL STUDIES IN THE CHENOPODIACEAE

I. INFLORESCENCE OF ATRIPLEX AND BASSIA

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[*Manuscript received March* 1, 1960]

Summary

Anatomical techniques were employed to explain the morphology of the inflorescence of certain Australian species of *Atriplex* L. and *Bassia* All. Clearing of tissues by chlorallactophenol was used extensively and proved to be superior to the slow conventional method of sectioning and reconstruction.

Vascularization of the stem and the inflorescence was studied and described. It was found that the inflorescences of *Atriplex* are of two types. One is terminal in origin; and the second is axillary, containing female flowers, and is complex, being a much-condensed form of compound dichasium. The lateral branches of such an inflorescence are always dichasia of female flowers, but the terminal branch is variable and can be either a male dichasium, a female flower, or a vegetative shoot.

The solitary flower of *Bassia* is derived from the suppression of the lateral branches of such an inflorescence and a reduction in the number of flowers in the terminal branch. Two species of *Bassia*, however, bear an inflorescence which is a condensed dichasium.

Attention is drawn to the similarity of the vascular system of the male inflorescence of *Atriplex* and the primary vascular system of the *Bassia* stem.

The development, morphology, and anatomy of the fruiting bracteole of *Atriplex* is described in some detail and it is concluded that it is a true bracteole.

I. Introduction

Our knowledge of the morphology and anatomy of the members of the family Chenopodiaceae indigenous to Australia is meagre. All of the previous work (Wood 1923; Moser 1934; Black 1954) dealt with the anatomy of the leaf, especially that of *Atriplex* L.

This paper presents the results of an investigation of the nature of the inflorescence in *Atriplex* L. and *Bassia* All. The vascularization of both vegetative and flowering organs has been studied by anatomical techniques, especially the clearing of whole organs. Special attention was paid to the morphology and anatomy of the fruiting bracteole of *Atriplex*, the true nature of which had been somewhat in doubt.

II. Material and Method

(*a*) *Material*

Atriplex species (Australian) selected for this work were *A. angulata* Benth., *A. lindleyi* Moq., *A. inflata* F. Muell., *A. vesicaria* Hew. ex Benth., and *A. spongiosa* F. Muell.

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Bassia species (Australian) were *B. longicuspis* F. Muell., *B. ventricosa* J. M. Black, *B. paradoxa* (R.Br.) F. Muell., and *B. biflora* var. *cephalocarpa* F. Muell.

Inflorescence material was collected late in May 1958 from the University of New England Research Station at Fowler's Gap, about 70 miles north of Broken Hill, N.S.W., and preserved in formalin-acetic-alcohol.

(*b*) *Methods*

In studying the vascular system, gross clearing of the relevant parts was found more satisfactory than the method of reconstruction from serial sections. The following clearing methods were tried:

(i) Lactic acid solution in water, after Simpson (1929), was used. The result was quite satisfactory but only after several weeks of treatment.

(ii) Pure lactic acid in a water bath, as suggested by Sporne (1948) was also successful, but was abandoned in favour of a modified chlorallactophenol method which proved to be the best for this particular material.

(iii) Chlorallactophenol was used as recommended by Vautier (1949) (2 parts chloral hydrate, 1 part carbolic acid, 1 part pure lactic acid with gentian violet to differentiate the tissues). Treatment was carried out in an incubator at 56°C, for 2–3 hours. Vautier used this method of clearing after a process of depigmentation and bleaching by chlorine. The whole process was carried out quite successfully on both *Atriplex* and *Bassia* material, but it was found that the time of treatment could be cut more than tenfold if the method shown below was employed.

(iv) The method adopted was as follows. After fixation in formalin-acetic-alcohol, material was treated with chlorallactophenol (1 part chloral hydrate, 1 part white carbolic acid, 3 parts pure lactic acid). This solution is less dense than that of Vautier, but the refractive index is excellent. Material of various sizes (from a single flower or fruit to a shoot of up to 10 nodes) was dropped into test-tubes containing chlorallactophenol, and these were corked and put into a water bath kept at boiling point, or into a sand bath kept at the same temperature. Owing to the density of the liquid, the material at first floated, and this served as an excellent guide to time the treatment required. After 10–30 min, according to the nature of the material, it started to sink, which indicated that it was ready for further dissection and observation. The dense vesicular layers and the pigmented layers of the cortex obscured the internal structure to some extent, but these outer tissues could be peeled off readily.

The clearing effect of chlorallactophenol on the unlignified tissues is excellent; the lignified tissues are left as white continuous strands, and the necessity for depigmentation and staining is eliminated altogether.

For studies of the development of flowers and buds and the vascular system of minute organs, conventional paraffin sections were cut at 10–15 μ and stained in safranin-fast green.

III. Inflorescence Morphology

(*a*) *Atriplex*

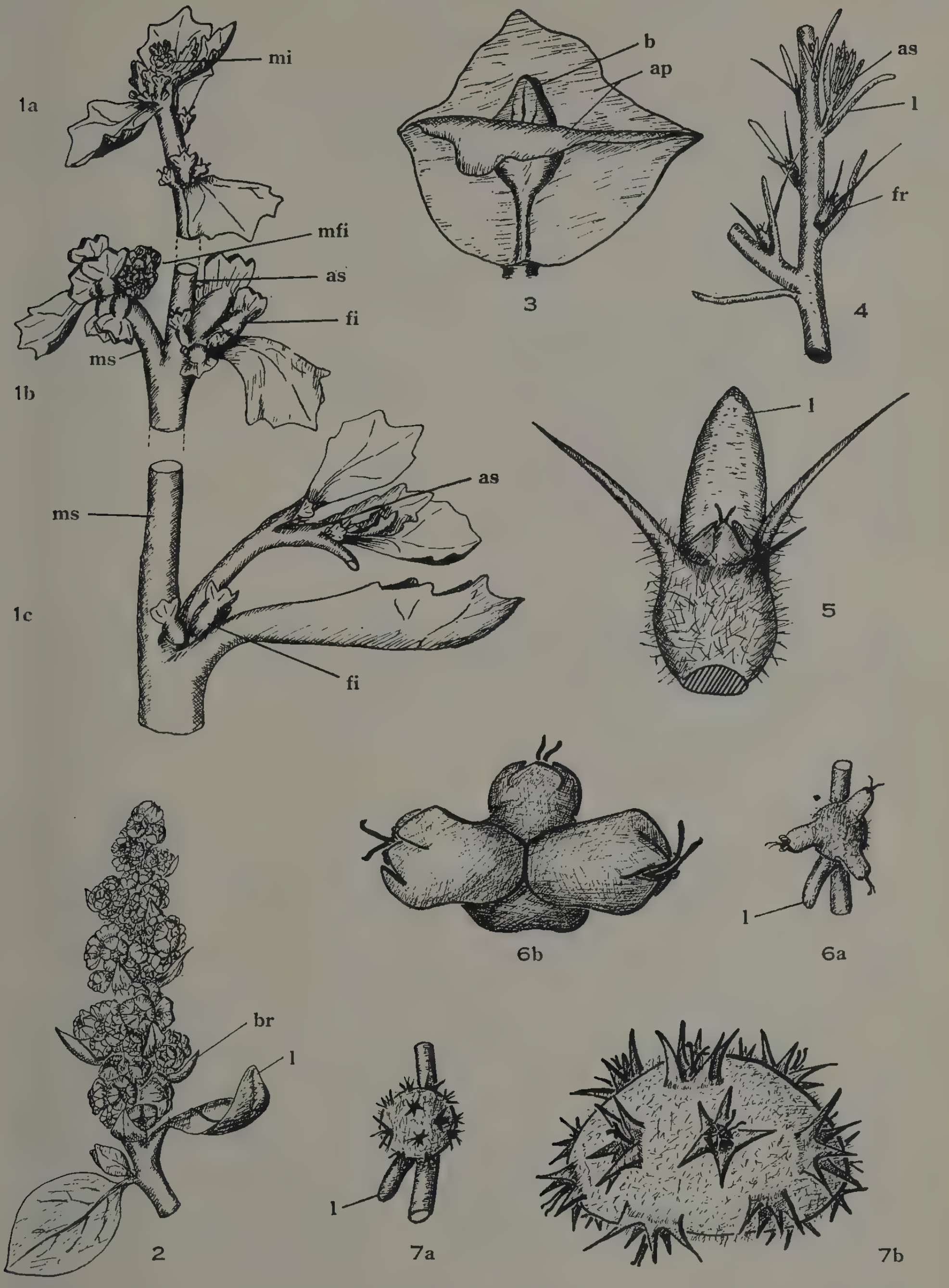
During the period of active growth the *Atriplex* plant shows pronounced sympodial growth (Fig. 1). The male inflorescence is always terminal and is a spike of dichasia (Figs. 1, 2) in which the subtending bracts have a phyllotaxy of 2/5. In the monoecious species the spike is much condensed (Fig. 1*a*). The female cluster is always axillary and arises from a cushion-like, fan-shaped region on the adaxial side of the leaf base. There is no common peduncle and the pedicles arise independently directly from the cushion. The number of flowers in a cluster varies from two to eight, *A. angulata* and *A. intermedia* being notable for the occurrence of the largest number (clusters of six to 10 or more are common). The oldest flowers are found nearest to the main shoot, and the order of flowering proceeds centrifugally.

If the female cluster and an axillary shoot arise from the same axil, the shoot is always situated in a median position between the cluster and the main axis. The cluster has, in fact, assumed the position of an accessory branch at this node (Fig. 1*c*). Mixed flower clusters (male and female), if axillary, are never accompanied by an axillary shoot, and if they occur terminally they appear to be subtended by a normal leaf (Fig. 1*b*). There are only a few female flowers, usually two to four, on the lower part of such a cluster.

In the dioecious *A. vesicaria* the pattern is not so intricate. Female plants have inflorescences only at their nodes, and the terminal apices remain vegetative. The male inflorescences in the male plant, as a rule, are terminal, but occasionally normal female flowers were found on the axils and in a few cases there is no alternative but to call the plant monoecious.

As far as is known no work has been done on the nature of the *Atriplex* inflorescence. Most authorities (Bentham 1870; Willis 1931; Black 1948) refer to the inflorescences, particularly the female ones, as "flower clusters". Bentham described the *Atriplex* inflorescence as: "male flowers in globular clusters, either detached from the females in close or interrupted simple or paniculated spikes, or axillary and then each cluster usually surrounded by females; female flowers usually in axillary clusters, rarely solitary or the clusters in terminal leafless panicles". Willis described the inflorescence of the family Chenopodiaceae as: "often primarily racemose, but the partial inflorescences are always cymose, at first often dichasial, but with tendency to cincinnus form". Black described the male inflorescence as being a cluster, a spike, or paniculately arranged in short spikes. Every authority noted the occurrence of mixed clusters, i.e. the occurrence of male and female flowers together in a cluster.

Perhaps the study of the external morphology of the inflorescence justifies the use of the term "cluster", and the order of flowering which proceeds centrifugally suggests that the infloresence could be cymose, but one can not proceed further than that on morphology alone. It became evident, therefore, that the vascularization at nodes and extremities would have to be studied in elucidating this problem.



Figs. 1–7.—Morphology of *Atriplex* and *Bassia* inflorescences. Figs. 1*a*–1*c*.—Occurrence of various types of inflorescence of *Atriplex intermedia*. ×2. Fig. 2.—Male inflorescence of *Atriplex vesicaria*. ×4. Fig. 3.—Fruit of *Atriplex lindleyi*. ×5. Fig. 5.—Fruit of *Bassia ventricosa*. ×6. Figs. 6*a*, 6*b*.—*Bassia biflora* flowers. Figs. 7*a*, 7*b*.—*Bassia paradoxa* flowers. *ap*, Appendages; *as*, axillary shoot; *b*, bracteole; *br*, bract; *fi*, female inflorescence; *fr*, fruit; *l*, leaf; *mi*, male inflorescence; *mfi*, mixed flowered inflorescence; *ms*, main shoot.

(*b*) *Bassia*

The majority of the Australian species of *Bassia* bear a solitary flower at the nodes of the plant (Fig. 4). *B. biflora* and *B. paradoxa*, however, bear an inflorescence of two to three and six to 10 flowers respectively. In all cases the bases of the floral tubes are fused together into a head (Figs. 6, 7).

IV. Floral Morphology and the Fruiting Bracteole

Atriplex flowers are unisexual with five perianth segments in the male flowers, obdiplosteminous stamens, and a vestigial ovary. Female flowers have two opposite and persistent bracteoles which undergo post-fertilization changes to become the fruiting bracteoles. These form a conspicuous structure which is taxonomically important. The bracteoles are leaf-like in appearance and may fuse to form a tube, or remain free almost to the base. The distal portion is green and reticulately veined and covered with vesicular tissue; and many species, such as *A. vesicaria*, *A. inflata*, and *A. spongiosa* have an appendage developed on each bracteole (Fig. 3). The androecium is absent and the ovary unilocular, with two styles.

The interpretation of the fruiting bracteoles of *Atriplex* has been a matter of controversy. It has been suggested that they are a pair of bracts borne on the pedicel of the flower, or a pair of modified perianth segments. The writer was of the opinion that this specific problem could be answered only by an investigation based on their morphogenesis and, particularly, the vascularization of both the flower and the bracteole itself. The definitions of the terms "bract" and "bracteole" also need to be considered.

Rickett (1954), in reviewing the meaning of these two terms, defined "bract" as "any leaf or leaf-like structure or scale which differs from the foliage leaves and which is associated with flowers or a flower". He then added: "it would seem idle to attempt to formulate the definition of bracts which excluded 'bracteole' ". He also suggested that "bracteole" should be defined "in the sense of the prophyll", which would mean, as he stated, "the lateral organs on individual pedicels".

Moquin-Tandon (1840) was the first to describe the two valves of the female flowers of *Atriplex* as bracteoles. Bentham (1870), having considered the insertion and development of the bracteoles, was of the opinion that they were homologous with the male perianth, and thus called them "fruiting perianths". Anderson (1930) used the term fruiting bracteole in his notes on the Australian species. Ulbrich (1934) concluded that the structure was a bracteole, but Aellen (1938) followed Bentham in describing it as a fruiting perianth. Black (1948) described the female flowers of *Atriplex* as having no perianth and applied the term bracteole to this structure.

Bassia flowers are bisexual and axillary. The perianth has five segments usually fused to form a floral tube with two to five spines arising from the proximal position (Fig. 5). The stamens are obdiplosteminous and the ovary unilocular, with two styles.

V. Ontogeny of the Inflorescence of Atriplex

(a) *The Structure of the Shoot Apex*

The apices of the vegetative shoots of all *Atriplex* species investigated resemble each other very closely. Each appears as a low, dome-shaped structure and bears four or five leaf primordia in close spiral succession, each new primordium originating as a slightly raised protuberance on the flank of the apex. The height of the apex above the youngest leaf primordium varies from 25 to 40 μ. The adult apex has three tunica layers (Fig. 8), the innermost (t_3) showing frequent periclinal divisions, but generally the three-layered appearance is quite distinctive. The central and peripheral regions of the corpus were recognized and the rib meristem appeared at approximately four layers of cells below the tunica layers. Black (1954) investigated the ontogeny of the leaves of *Atriplex* species, and gave a schematic representation of tissue differentiation and the other detail of the development of the leaves. The present work confirms these findings; and it seems that the contribution of the corpus to the development of the leaf is restricted to the area at the base of the leaf.

(b) *The Initiation and Development of the Axillary Bud*

The axillary bud appears very early, close to the shoot apex, and seems to be derived from the residual meristem. In the early stages of development there is little difference in the appearance of vegetative and floral primordia. The first axillary bud, if it does not terminate directly in the floral apex, develops very rapidly into a vegetative shoot. Figure 9 shows the organization of the vegetative bud. The first two leaves arise in a lateral position in relation to the main stem, and are almost opposite (Fig. 10).

If the bud, on the other hand, terminates as a female flower, only two tunica layers are found (Figs. 11, 12). The two opposite bracteole primordia arise early on the flank of the hemispherical bud. The development of the bracteole primordium follows closely the development of the leaf primordium, starting with the periclinal division of t_2. Here again the corpus has little to do with the formation of the bracteoles. The marginal initial is derived from t_1 of the bud, and the submarginal cell which gave rise to the inner structure of the bracteole is derived from t_2 (Fig. 12).

Anticlinal divisions at the base of the first axillary bud delimit the position which initiated the first two younger lateral bud primordia. Figure 11 shows the initiation of one such bud in relation to the first bud. Two groups of meristematic cells on each side of its base, but slightly to the abaxial side, start to divide rapidly. The first of the two younger bud primordia appears at about the same time as the bracteole primordia on the first bud. These two younger buds are to be developed into the first two lateral flowers of the dichasium, but if the first axillary bud develops vegetatively, they become the first two terminal flowers described below (Section VI(*a*)(ii)). This pattern of dichasial branching of lateral buds is repeated several times in many-flowered species such as *A. angulata* and *A. intermedia*.

Figure 13 shows the development of the vascular system, which starts from that of the terminal bud and appears to proceed acropetally into the younger bud.

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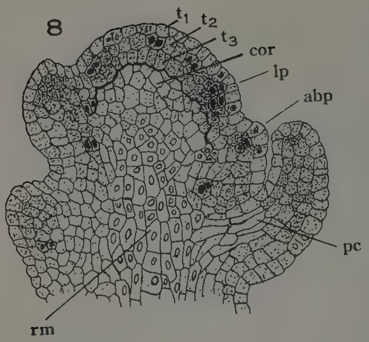
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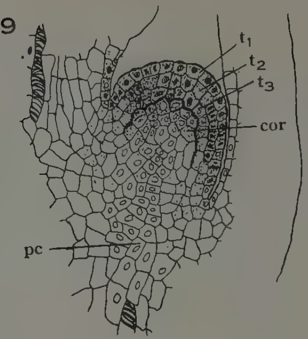
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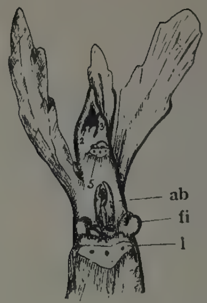

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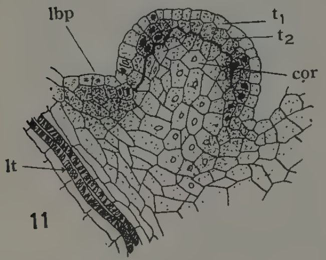
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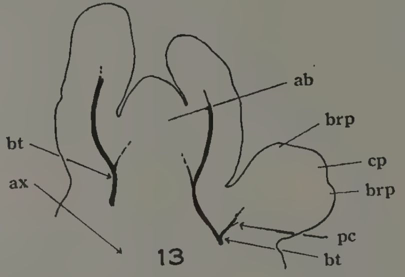
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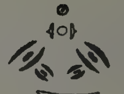

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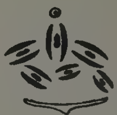

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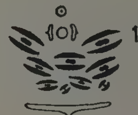

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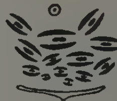

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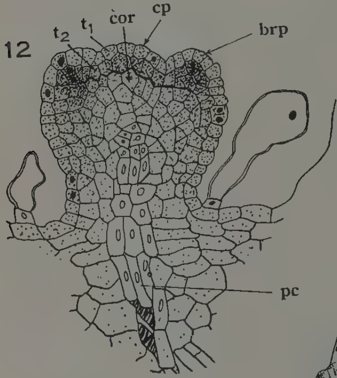
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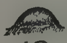

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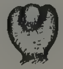

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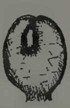

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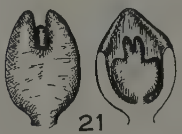

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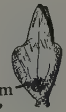

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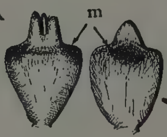

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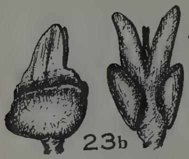

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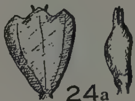

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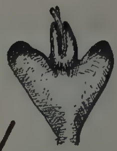

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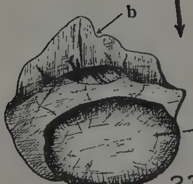

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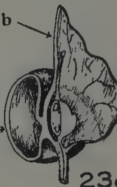

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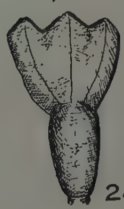

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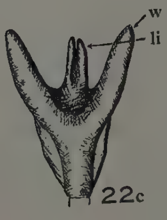

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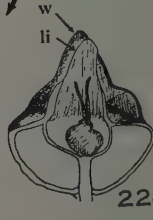

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(*c*) *Orientation of the Bracteole*

As stated above, the first two leaves of the axillary shoot are oriented laterally in relation to the main axis (Figs. 10, 14). On the other hand, if the axillary bud terminates in a female flower the two opposite bracteoles are similarly oriented (Fig. 15). However, the fully developed bracteoles of the first and terminal flowers in the inflorescence of the bilaterally symmetrical *A. lindleyi*, *A. inflata*, and *A. vesicaria* become posterior–anterior, or almost so, as the result of the twisting of the pedicels. Such twisting does not occur, or is rare, in *A. spongiosa*, mainly because of the radial symmetry of its fruits. This suggests that twisting of the pedicel only occurs when there is a problem of available space in the axil. The pattern of the orientation of the bracteole is repeated in the lateral flowers of the inflorescence in relation to the terminal flower or the axillary shoot (Figs. 16, 17).

(*d*) *Differentiation of the Fruiting Bracteole*

Figures 18–21 show successive stages in the development of the flowering bracteoles before differentiation sets in. The six species investigated can be grouped, according to the differentiation of the fruiting bracteoles, into those with appendages on the bracteoles, e.g. *A. lindleyi*, *A. vesicaria*, *A. inflata*, and *A. spongiosa*, and those without appendages, e.g. *A. intermedia*, *A. angulata*, and occasionally *A. vesicaria*. Prior to fertilization, the young flower assumes a tear-drop shape with two more or less obtuse bracteoles joining half way up, forming a cup-shaped structure enclosing the carpel (Fig. 21). Development from this stage into a mature bracteole is accelerated after fertilization, and follows closely the pattern of foliar differentiation. Apical and subapical growth is followed by marginal growth at the base. Development of the appendages, which occurred in four species investi-

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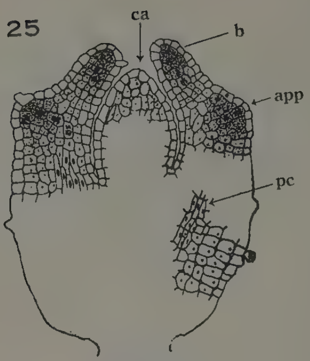
Figs. 8–13.—Sections of *Atriplex intermedia*. Fig. 8.—Longitudinal section of the stem apex. ×120. Fig. 9.—Median longitudinal section of a vegetative axillary bud. ×120. Fig. 10.—Shoot apex and the upper nodes. ×10. Fig. 11.—Longitudinal section of a flower primordium. ×120. Fig. 12.—Median longitudinal section of an older flower primordium. ×120. Fig. 13.—Development of the procambium of young buds. ×120. Figs. 14–17.—Diagrams showing the orientation of the bracteole of *Atriplex*. Fig. 14.—Orientation at a node containing an axillary branch. Fig. 15.—Orientation at a node without an axillary branch. Figs. 16, 17.—Orientation at nodes of the many-flowered species with and without axillary branch respectively. Figs. 18–24.—Development and differentiation of the bracteoles and their appendages of *Atriplex*. ×15. Fig. 18.—Flower primordium, Figs. 18–21.—Early stages in the development of the flower bud up to the tear-drop stage of development, with half-flower diagram (Fig. 21). Figs. 22*a*–22*c*.—Development of the bracteoles and their appendages in *A. lindleyi*. ×3. Figs. 23*a*–23*c*.—Development of the bracteoles and their appendages in *A. vesicaria*. ×3. Fig. 23*d*.—Quarter-flower of *A. vesicaria*, showing the bracteole and its appendage. ×3. Figs. 24*a*, 24*b*.—Development of the bracteole of *A. intermedia*. ×3. *ab*, Axillary bud; *abp*, axillary bud primordium; *ap*, appendages; *ax*, axis; *b*, bracteole; *brp*, bracteole primordium; *bt*, branch traces; *cor*, corpus; *cp*, carpel primordium; *fi*, female inflorescence; *l*, leaf; *lbp*, lateral bud primordium; *li*, lip (tip of bracteole); *lp*, leaf primordium; *lt*, leaf trace; *m*, meristematic regions; *pc*, procambium; *rm*, rib meristem; t_1, t_2, t_3, tunica layers; *w*, wings (appendages); *2*, *3*, *5* (Fig. 10), number of leaves under the apex.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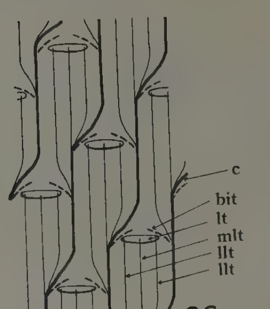
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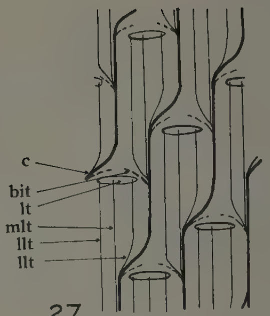
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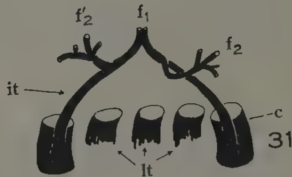
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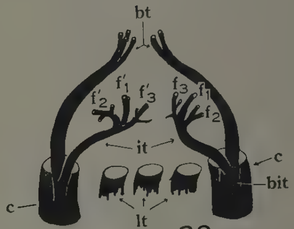
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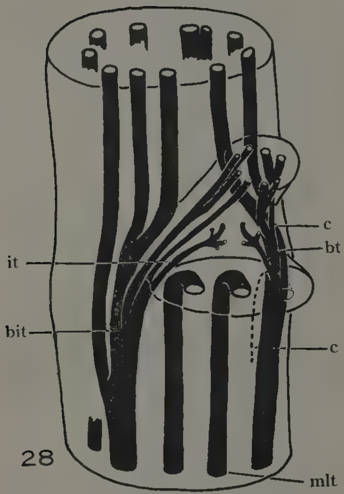
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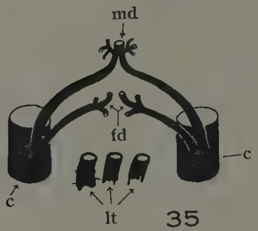
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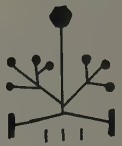
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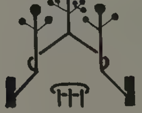
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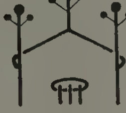
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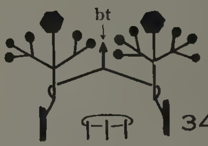
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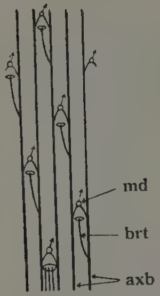
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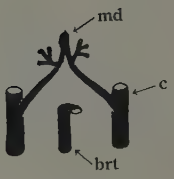
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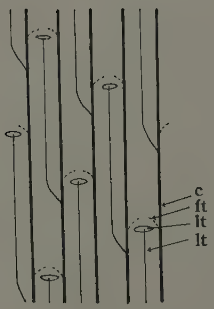
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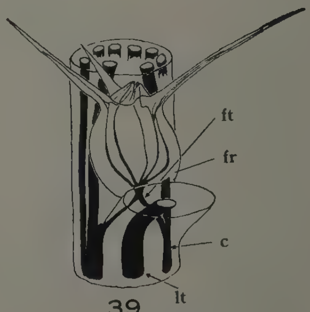
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Fig. 25.—Longitudinal section of *A. lindleyi* flower bud. Figs. 26–28.—Primary vascular system of *Atriplex*. Fig. 26.—Primary vascular system of *A. spongiosa*. Fig. 27.—Primary vascular

[*For continuation see opposite page*]

gated, is the result of localized meristematic activities on the bracteole during differentiation.

The appendages of *A. lindleyi*, *A. inflata*, and *A. spongiosa* resemble each other very closely in their development. A group of meristematic cells located about two-thirds of the way along the median plane of each bracteole divides in the pattern of the growing bud, i.e. anticlinally on the surface and periclinally internally (Fig. 25). It grows outwards and upwards in a similar manner to the development of the leaf primordium, and at a faster rate than the tip of the bracteole itself, becoming a structure known as a "wing" in *A. lindleyi* and *A. inflata* (Figs. 22*a–d*). The wing of *A. inflata* is somewhat flatter and slightly different in vascular structure from that of *A. lindleyi* (see below). The meristematic activities of the bracteole of *A. spongiosa*, on the other hand, are not confined to a particular area as in previous cases. A concentric band of meristematic cells is found below the level of the fusion of the two bracteoles, and as a result of its activities a concentric globular appendage is formed enclosing almost entirely the original bracteole, which can be identified upon dissection (see below).

Generally *A. vesicaria* has an appendage developed on the lower portion of the bracteole. A localized meristematic zone appears near the base of the bracteole, above the median vascular bundle (Figs. 23*a–d*). Development is rapid, and a balloon-like structure is found covering most of the lower part of the bracteole (Figs. 23*c*, *d*), but occasionally this appendage is absent.

A. intermedia and *A. angulata* have no appendage and the bracteole is differentiated in the foliar pattern. During their differentiation the pedicels also elongate rapidly, and in mature fruits the carpel chamber is pushed upward from the cushion of the leaf axil (Figs. 24*a*, *b*).

VI. VASCULARIZATION

(*a*) *The Inflorescence of* Atriplex

Esau (1954) defined the primary system as consisting of those vascular tissues which have their inception during the growth of the primary plant body.

All figures presented here are drawn from the upper part of the plant in which anomalous secondary thickening has yet to appear. Two types of figures are given.

Figs. 25–39 (*Continued*)

system of *A. angulata*. Fig. 28.—Vascularization at node of *Atriplex*. Figs. 29, 30.—Vascular system of male inflorescence of *Atriplex*. Figs. 31–37.—Diagrams showing vascularization of various types of *Atriplex* inflorescence. Fig. 31.—Vascularization of an axillary female dichasium. Fig. 32.—Vascularization of an axillary inflorescence which has two lateral female dichasia and a terminal vegetative branch. Figs. 33, 34.—Diagrams of inflorescences shown in Figs. 31 and 32 respectively. Fig. 35.—Vascularization of an axillary mixed flower inflorescence. Figs. 36, 37.—Diagrams showing axillary and terminal mixed flower inflorescence respectively. Figs. 38, 39.—Primary vascular system of *Bassia*. Fig. 38.—Longitudinal course of the primary vascular system. Fig. 39.—Vascularization at node of *B. ventricosa*. *app*, Appendage primordium; *axb*, axis vascular bundle; *b*, bracteole; *bit*, branch or inflorescence trace or both; *brt*, bract trace; *bt*, branch trace; *c*, cauline bundle; *ca*, carpel; f_1, f_2, . . ., flowers in order of age; *fd*, female dichasium; *fr*, fruit; *ft*, floral trace; *it*, inflorescence trace; *llt*, lateral leaf traces; *lt*, leaf traces; *md*, male dichasium; *mlt*, median leaf trace.

One represents diagrammatically the longitudinal course of the primary vascular system in one plane, the cauline bundles being indicated by heavy lines and the foliar bundles by thin lines. At the nodes the positions of leaf bases are shown as narrow elliptical structures, and the broken lines represent branch or inflorescence traces or both. The second type of figure was drawn from what was actually observed under a stereomicroscope after the tissues had been cleared and dissected.

The longitudinal course of the primary vascular system of *Atriplex* shows no significant difference between species. There are 10 or 11 vascular bundles in the stem, the variation being due to a slight difference in the level of origin of the median bundle of the leaf traces. There are normally three cauline and seven or eight foliar bundles (Figs. 26, 27).

Nodes of both *Atriplex* and *Bassia* are unilacunar, a characteristic of the family (Sinnott and Bailey 1914). Within the node of *Atriplex* each of the two cauline bundles on either side of the leaf gap give off three or four bundles. Of these, the one closest to the leaf gap supplies the axillary branch or inflorescence or both. If the axillary shoot and the inflorescence are found at the same node, the inflorescence trace branches off from the branch trace early in its course. The other branches of each cauline bundle continue their course up the stem (Figs. 26–28).

(i) *The Male Inflorescence.*—The vascular system of the male inflorescence confirms the external observations. From the typical vascular system of the stem there is a transition to that of the male inflorescence. After the uppermost leaf trace has departed from the axis there are altogether five vascular bundles running up the axis of the inflorescence (Fig. 29). This is the result of the branching of two of the original three cauline bundles of the stem. The third cauline bundle passes up the axis unbranched. Figure 30 shows that each dichasium in turn received its vascular supply from the two traces on either side of the trace of the subtending bract. These two traces join and supply the terminal flower. The two lateral flowers are supplied by traces from the base of the terminal flower and so on, in typical dichasial pattern. Each of the five bundles in turn terminates in a dichasium at the tip of the inflorescence. The subtending bract of the dichasium is supplied by a small strand given off from one of the five axis bundles just below the dichasium (Fig. 29).

(ii) *The Female Clusters.*—When a female cluster occurs alone at a node, the vascular system is of a simple dichasial type. The terminal flower arises in the median position nearest the main axis. The two vascular traces supplying this terminal flower correspond to the branch traces given off by the two cauline bundles at the node in the manner previously described. From the base of this terminal flower two female inflorescences develop and are supplied by vascular bundles branching in a dichasial manner from the terminal flower. Branching proceeds centrifugally and the youngest flowers are found furthest from the terminal flower (Fig. 31).

If a female cluster is accompanied by an axillary shoot, the inflorescence traces branch off from the branch traces and terminate in two lateral inflorescences.

Each is a typical dichasium, and they are located on either side of the axillary shoot (Fig. 32). Occasionally the secondary or tertiary traces of these two lateral inflorescences meet and run into a third, still younger, dichasium. In other words, there can be two or occasionally three dichasia of female flowers at a node, accompanying an axillary shoot. Types of female inflorescence most common in *Atriplex* are shown in Figures 33 and 34.

(iii) *The Mixed Flower Clusters.*—These clusters, as mentioned before, are either axillary or terminal; their vascular systems are similar, and show that the mixed flower cluster is not a simple inflorescence but consists of a terminal male and two lateral female inflorescences developed in very close proximity (Fig. 35). The male inflorescence is much condensed, and gives the impression of being the upper part of the mixed flower cluster.

In the axillary cluster the male inflorescence takes the position usually occupied by the axillary shoot, and vascularization shows that both male and female inflorescences branch off in typical dichasial pattern (Fig. 36).

The terminal mixed flower clusters are found to be similar in nature. The female inflorescence is again axillary in origin and the male terminal. Here the shoot apex terminates immediately above the node, in a condensed male dichasium. In such a condition, therefore, the clusters are always subtended by the leaf of the last node (Fig. 37).

(*b*) *The Inflorescence of* Bassia

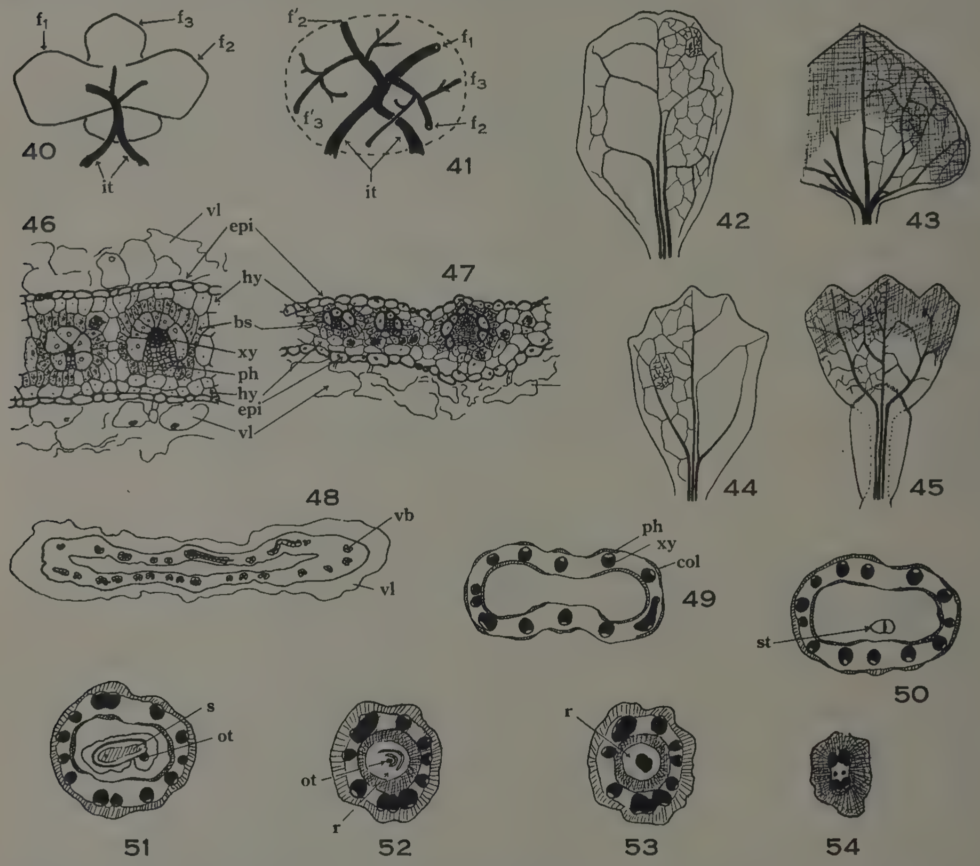
The primary vascular system of *Bassia* is much simpler than that of *Atriplex*. There are altogether eight or nine bundles at the internodes, and the number of cauline bundles is five (Fig. 38).

Attention must be drawn to the striking resemblance of the vascular system of the male inflorescence of *Atriplex* to that of the primary vascular system of the *Bassia* stem (Figs. 29 and 38 respectively). A further investigation into this matter may throw light on the relationship between these genera.

The condition at the node is much simpler in *Bassia*, because axillary shoots and inflorescences are never found together at the same node. Either organ is supplied by two traces from the cauline bundles on either side of the leaf gap (Fig. 39). The *Bassia* flower is, as a rule, solitary at each axil, but *B. biflora* and *B. paradoxa* bear more than a single flower at the nodes. The bases of the floral tubes fuse to form a head. There are two or three flowers per head in *B. biflora* and six to 10 in *B. paradoxa*. Vascularization reveals that these are also dichasial in nature. (Figs. 40, 41.)

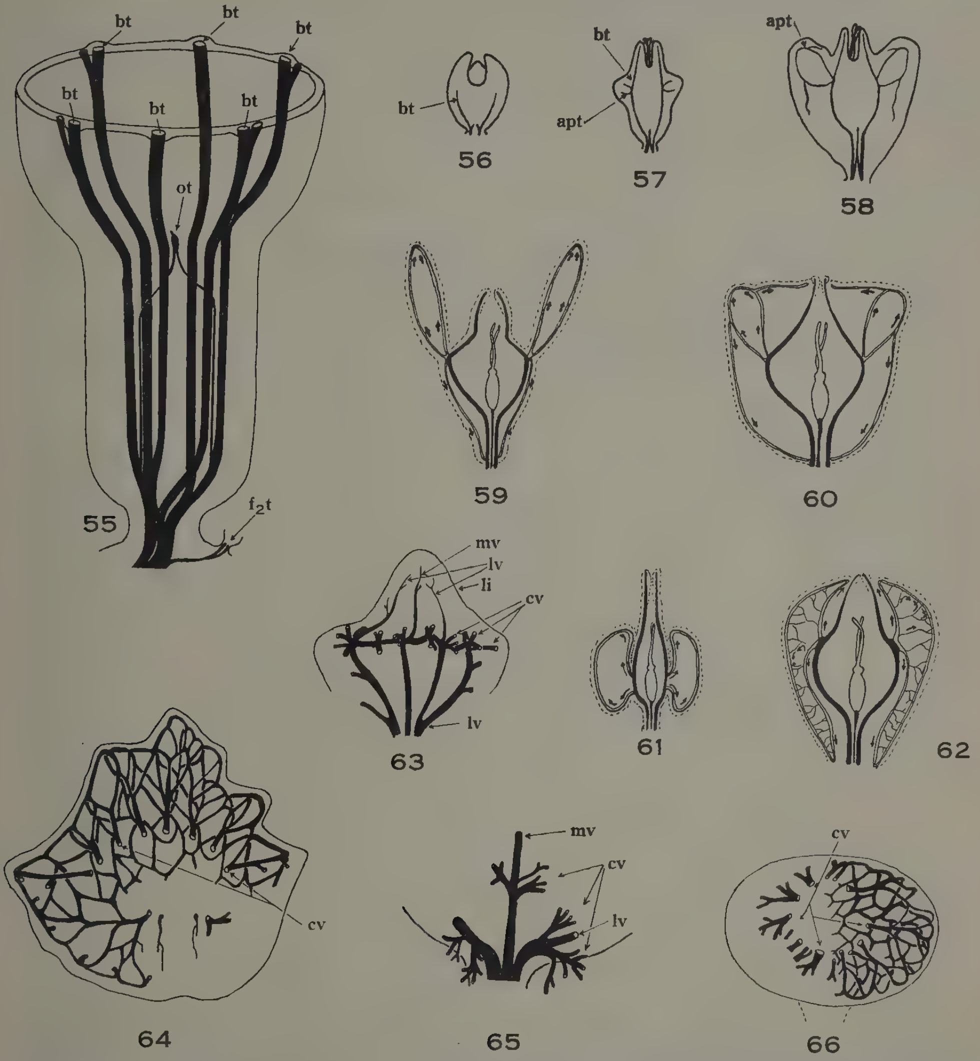
(*c*) *The Vascular System and Anatomy of the Bracteole of* Atriplex

Morphologically, bracteoles closely resemble the leaves of the same species, and apart from the occurrence of the appendages in certain species, there is no apparent difference between the two structures. The venation of the bracteole and leaves of the same species of *Atriplex* are not unalike in general outline (Figs. 42–45). The number of vascular bundles at the base of the bracteole is three, and the branching off of lateral veins resembles closely the pattern in the leaf. The vein islets of the two structures are also alike. Transverse sections of the green part of the bracteole agree with Black's (1954) anatomical description of the leaf. Thick vesicular layers are present, and below the epidermis there are one or two layers of hypodermal cells which are enlarged storage cells and contain few chloroplasts. The "Kranz" type of assimilatory tissue found in the leaf is also conspicuous here, and the bracteole is similarly isobilateral in structure. Figures 46 and 47 show the structure of bracteole and leaf respectively.



Figs. 40, 41.—Vascularization of *Bassia* inflorescence. Fig. 40.—*B. biflora*. Fig. 41.—*B. paradoxa*. Figs. 42–45.—Venation of leaves and bracteoles of *Atriplex*. ×3. Figs. 42, 43.—Venation of *A. vesicaria* leaf and bracteole respectively. Figs. 44, 45.—Venation of *A. intermedia* leaf and bracteole respectively. Figs. 46, 47.—Transverse sections of leaf and bracteole of *A. intermedia* respectively. ×120. Figs. 48–54.—Serial transverse sections of *A. intermedia* fruit from the distal end towards the pedicel. ×10. *bs*, Bundle sheath; *col*, collenchyma tissues; *epi*, epidermis; f_1, f_2 . . ., flowers in order of age; *hy*, hypodermis; *it*, inflorescence trace; *ot*, ovary traces; *ph*, phloem; *r*, receptacle; *st*, stigma; *vb*, vascular bundle; *vl*, vesicular layers; *xy*, xylem.

Figures 48–54 are transverse serial sections of the young fruit below the green part of the bracteole. Here the "Kranz" structure disappears, and collenchyma is found under the epidermis and especially in the area above and below the vascular bundles. Parenchyma makes up the ground tissue in the central layers.



Figs. 55–66.—Vascularization of fruit of *Atriplex*. Fig. 55.—Vascularization of fruit of *Atriplex intermedia*. Figs. 56–58.—Early stages in the development of the vascular system of bracteole and its appendages in *A. lindleyi* and *A. inflata*. Figs. 59–62.—Development of vascular system of the appendages of *A. lindleyi*, *A. inflata*, *A. vesicaria*, and *A. spongiosa* respectively; arrows show direction of development of procambium in the appendages. Figs. 63–66.—Vascular network of the appendages, and its connexion with that of the bracteole. Figs. 63, 64.—*A. lindleyi*. Figs. 65, 66.—*A. vesicaria*. *apt*, Appendage trace; *bt*, bracteole traces; *cv*, connecting veins between appendages and bracteole vascular network; *ft*, younger flower trace; *lv*, lateral vein of bracteole; *mv*, median vein of bracteole; *ot*, ovary traces.

The vascular bundles in the pedicel become divided early in their course; at the base these consist of two bundles which subdivide again immediately, each giving rise to four bundles. Three of these are bracteole traces and the much smaller one is the ovary trace. The number of vascular bundles in the upper pedicel remains eight (Fig. 55). Each bracteole receives three bundles, and the remaining two supply the carpel. Transverse sections cut at the upper part of the pedicel, immediately underneath the ovary, show the demarcation of the receptacle tissue from that of the pedicel. In the receptacle tissue run the two ovary traces, which, as mentioned above, separate early from the bracteole traces and pass up practically the whole length of the pedicel to the interior of each of the three bracteole traces. These unite with each other and subsequently supply the ovary. (Fig. 55.)

In connexion with the development of the appendage of the bracteole of some *Atriplex* species described above, a brief mention should be made of their vascular system. In *A. lindleyi* and *A. inflata*, after the appendages are initiated by the localized meristem two procambial strands are found to develop acropetally from the main vein into the developing wings, one toward its upper surface, the other toward the lower (Figs. 56–58). The development and course of the vascular system of these appendages of the four species mentioned previously are shown in Figures 59–62. Arrows indicate the direction of the development of the procambium in the appendages, and the thick lines show the course of the median traces of the bracteole as seen in median section from the pedicel to the tip of the bracteole. In *A. lindleyi* and *A. vesicaria*, most of the lower parts of the bracteole are covered by appendage tissues. In *A. spongiosa* and *A. inflata*, on the other hand, practically the whole of the fruit is covered with the appendage tissues, except the very tips of the bracteoles, which are known as "lips". The epidermal cells of the appendage cut off vesicular tissue, and this is shown as a broken line in the figures. Immediately underneath the epidermis lies a complex network of vascular tissues. The "Kranz" structure is characteristic of the assimilatory tissues of the appendage as well as that of the green portion of the bracteole. The network of the vascular tissue of the appendage and its connexion with the main veins of the bracteole of *A. vesicaria* and *A. lindleyi* are shown in Figures 65–66 and 63–64 respectively.

VII. Discussion

(*a*) *The Nature of the Inflorescence*

Parkin (1914) introduced the terms "intercalary" and "pseudo-terminal" in an attempt to explain the nature of the inflorescence of some plants such as the Australian *Callistemon*, *Drimys*, and *Boronia*. McLean and Ivimey-Cook (1956) defined intercalary inflorescences as those which "occur as zones in the development of the shoot, which continues its vegetative growth beyond them", and are originated as the result of the reduction of more extensive branch systems. A pseudo-terminal inflorescence, on the other hand, is derived from the suppression of the terminal branch of such an intercalary inflorescence, and as a result a group of axillary inflorescences become congested at the apex of the branch.

Before an attempt is made to interpret the nature of the inflorescence of *Atriplex* the present findings are summarized:

(i) The male inflorescence is always terminal and is a spike of dichasia.

(ii) At the axils of the upper leaves one of the following structures is found:

(1) A vegetative axillary shoot with female dichasia as its lateral branches.
(2) A terminal female flower with two lateral female dichasia.
(3) A terminal male inflorescence with two female dichasia as its lateral branches. This type of inflorescence could occur at a terminal position on a shoot as well as in an axillary position.

The study of inflorescence vascularization revealed that one could classify (ii)(1) as intercalary, or it could be interpreted as a type of compound dichasium with a terminal vegetative branch and two lateral branches of female dichasia. In the case of (ii)(2), the inflorescence is a typical dichasium with a terminal female flower. In (ii)(3) the terminal branch of the inflorescence terminates abruptly in a male dichasium, and again the two lateral branches are female dichasia. One could call this pseudo-terminal, or yet another type of compound dichasium different from that of the previous two cases.

The writer, however, prefers to simplify the matter by referring to these various types of inflorescence as varieties of a compound dichasium. In each case the two lateral branches are always dichasia of female flowers and the variation, therefore, lies entirely in the development of the terminal bud of the inflorescence. In (ii)(1) the terminal bud of the compound dichasium remains vegetative, but in (ii)(2) it differentiates into a female flower, and finally it may develop into a male dichasium as in (ii)(3). Occasionally the terminal bud is suppressed altogether and the inflorescence then consists of the two lateral dichasia of female flowers.

In *Bassia* the inflorescence is again a dichasium in *B. biflora* and *B. paradoxa*, but in the majority of species which bear an axillary flower at nodes, this is derived from the suppression of the lateral buds of the dichasium.

(*b*) *The Fruiting Bracteole of* Atriplex

The writer is of the opinion that the fruiting bracteoles are not homologous with the male perianth segments, as suggested by Bentham (1870). Ontogeny of the bracteole shows a typical foliar type of development from its initiation to the end of its differentiation. The orientation of the two bracteoles also corresponds to that of the first two leaves of the axillary vegetative bud, in that they are lateral in position in relation to the main axis. In the many-flowered species, the bracteoles are often found to be posterior–anterior in position, but this is believed to be due to the restriction of available space at the axil. Furthermore, each bracteole receives three bundles from the pedicel, while the male perianth receives but one. Another important point is that only the ovary traces pass through the receptacle tissue. These depart early from the bracteole bundles, to which they run parallel and internally up practically the whole length of the pedicel, diverging into the receptacle tissue, where they unite and supply the ovary.

The vascular system of the pedicel is, therefore, not unlike that of the stem. There are two sets of three bracteolar bundles, and the two ovary traces, which are comparable to the cauline bundles of the stem. Anatomical studies of the bracteole again show the similarity of the bracteole to the leaf.

The present evidence indicates that the fruiting bracteole of *Atriplex* is, in fact, a bract borne on the pedicel of the flower, and that the use of the term bracteole is justified.

VIII. Acknowledgments

The author wishes to express his sincere thanks and appreciation, especially to Associate Professor G. L. Davis for her valuable help and supervision in planning the work and preparation of the manuscript, and in going through it critically; to Professor N. C. W. Beadle, whose assistance throughout was most valuable; to Mr. J. B. Williams of the Botany Department, University of New England, for a great deal of assistance throughout the work; and to Dr. C. Barnard, Division of Plant Industry, C.S.I.R.O.

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SOME OBSERVATIONS ON THE LIFE HISTORY OF *PODOCARPUS FALCATUS*

By T. G. B. Osborn*

[*Manuscript received December* 18, 1959]

Summary

Podocarpus falcatus (R.Br. ex Mirb.) belongs to the 1-year life cycle type of podocarp. Ripe seeds are shed 12–13 months after pollination. There is a single gynospore mother cell in a well-defined tapetum, and the inner spore of a linear tetrad is functional. Pollen tubes make contact with the developing female prothallus before the stage of free nuclear division is complete. They continue to grow downwards between it and the nucellus. There are several superficial archegonia, some of which may be enveloped by a common jacket layer. They are of intermediate length, and develop along the line of contact between the pollen tube and prothallus. The gynospore layer membrane remains thin at this point. Five free mitoses of the zygote nucleus take place, the first two in the mid archegonial area. The proembryonic nuclei become tiered with a low number in the embryonic layer. The embryonic cells have the usual binucleate phase followed by tetrad formation. Simple polyembryony is common, and though fission may occur it is not general.

I. Introduction

Of late years the embryogeny of the different genera of the Podocarpaceae has aroused much interest among workers on conifer morphology. Unlike the embryogeny of members of the Pinaceae, in which there is considerable uniformity of "drill" amongst the nuclei, that of the podocarps shows great variability amongst the genera. Even in the genus *Podocarpus* itself the behaviour shows much diversity.

Buchholz (1941), whose revival of methods of dissection has thrown so much light upon conifer embryogeny (Buchholz 1938), particularly when fission polyembryogeny was involved, was quite defeated in his attempt to produce a general plan for the podocarps. He paid insufficient attention to the proembryonic stages, and failed to observe that in the development of the tiered embryo a variable number of the nuclei may be discarded. It was left to Doyle (1954) to present a satisfactory unity of plan within the large genus. Unfortunately he had insufficient information about members of the subgenus *Stachycarpus*. Imperfect as they are, the following observations on *Podocarpus falcatus* help to supply that deficiency.

II. Material

Podocarpus falcatus (R.Br. ex Mirb.) is a south-eastern African tree growing from Cape Province as far north as Portuguese East Africa. It grows well and seeds freely in Adelaide (lat. 35° S.) and in Sydney, but fails to reproduce in the Botanic Gardens at Melbourne (38° S.). The following observations refer to material collected from one female tree growing in the Botanic Park, Adelaide, checked from time to time against two other female trees growing in the Adelaide district.

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Female branch systems are borne axillary to the leaves, at the distal end of the false whorl of vegetative shoots which was formed the previous year below the terminal bud of a main shoot. Although generally only one branch system occurs in each axil it is not uncommon to find two. In such cases a reduced and non-functional vegetative bud occurs between them (Fig. 1). In South Australian material I have not found that both ovules mature, as figured by Stapf in the "Flora Capensis" (1933).

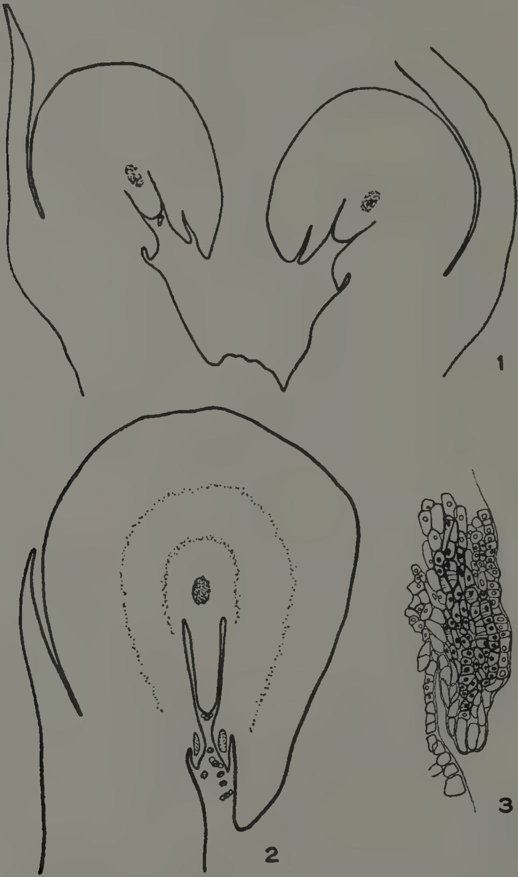


Fig. 1.—Longitudinal section of two female branch systems, showing an abortive vegetative bud between them. 4.x.1958. ×15. Fig. 2.—Longitudinal section of an ovule at time of pollination. Seven grains are within the micropyle. The closing tissue near the apex of the integument is stippled. 29.ix.1955. ×15. Fig. 3.—Closing tissue enlarged from Fig. 2, showing the nucleate thickened cells with fine striations and the regular cells lining the micropyle. 29.ix.1955. ×68.

The male branch systems are more widely spread along similar laterals on the pollen-bearing trees. In the Adelaide material it is not uncommon to find three branch systems in the axil of a leaf (Wilde 1944). Two occur about as frequently as a single one.

Pollination occurs in September to early October, depending upon the season. Brownlie (1953), in his study of the New Zealand podocarps, remarks that the time schedule is not strict there. Such is the case in regard to *P. falcatus* as observed in the Adelaide district during the past few years.

The ovules at pollination are roughly ovoid, 3 mm long and somewhat less in their widest diameter. They are subtended by several deciduous scale leaves, most of which fall early except the small scale subtending the ovule itself on the side remote from the micropyle (Fig. 2). In some ovules the aggregation of pollen grains in the micropyle is striking. Although the male trees within the Adelaide Botanic Park are growing several hundred metres from the female used as the chief source of material, and with many intervening trees of large size, as many as nine pollen grains have been counted in a micropyle under conditions of natural pollination. On the other hand, a much larger number of ovules fails to be pollinated at all and there is a heavy fall of such ovules early in November.

In *P. falcatus* there is no halt after pollination. The life cycle is of the single-year type (Doyle 1954), and ovule, pollen grain, and gynospore all continue their development without a pause. The large truncated cone of nucellar tissue, which forms a prominent feature within the integument, may reach a length of almost 1 mm. The upper end of the integument has well-developed "closing tissue" (Boyle and Doyle 1953). The deeper cells of this are lignified with fine transverse striations and prominent nuclei (Fig. 3). It appears possible that this tissue may be associated with local water secretion. It is covered on the micropylar surface with regular parenchyma cells. These resemble more the closing tissue of such ovules as those of *Callitris* or *Tetraclinis*, but make no inward growth closing the aperture as in those genera.

By the end of December to early January, the female prothallus has passed the alveolar stage and is firm enough to be dissected from the ovule. Sclerization of the inner portion of the integument has already begun, making sectioning of the whole ovule impracticable. Fertilization occurs towards the end of January, but archegonia, still undergoing development, may be found in the same prothallus as late as February, together with proembryos in various stages. By early March the sclerotesta is well developed. It becomes very hard and stony. The prothalli are best removed after it has been carefully cracked in the jaws of a vice. The outer covering (sarcotesta and epimatium) remains green and covered with a waxy bloom for some months longer. The inner layer of this is mucilaginous and contains much tannin. The sculpturing of the surface of the "stone" appears to be developed from the cells of this layer.

By August, the ovules, which have steadily increased in size and are now some 2 cm in diameter, become pale yellow and the outer portion is much softer. They resemble small spherical plums dangling at the end of the denuded fertile branch systems, which by this date have elongated to between 1 and 1·5 cm. Ovules in this stage may hang upon the tree long after the pollination of the next season's crop. Although there is no halt in development the later stages of embryogeny are slow. The last ripe seeds usually fall during December. They contain embryos about 3 mm long, showing cotyledons only 0·5 mm long and embedded in an endosperm that contains oil and but little starch.

III. Results

(*a*) *The Male Gametophyte*

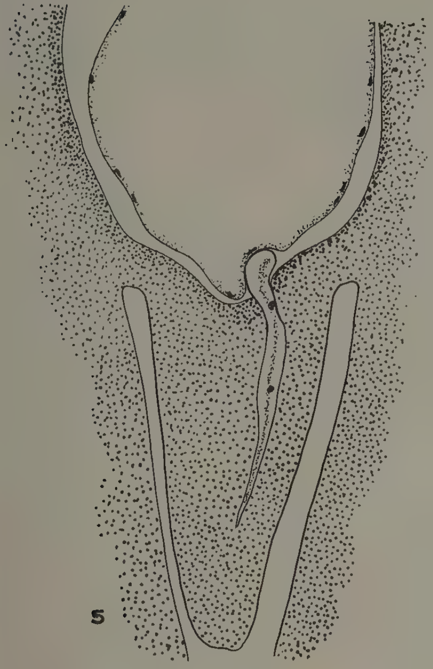
Pollen grains, as observed in the micropyle (September 29) stain very densely, and it is generally difficult to recognize more than two nuclei, the prothallial group and the tube and generative nuclei lying close together and appearing as one. However, some favourable preparations show that there are two prothallial nuclei and that tube and generative nuclei can be separated. The grains contain much starch (Burlinghame 1908). Germination follows shortly after contact with the nucellus beak (Fig. 4), but progress down its length, 0·8–0·9 mm, is not rapid. The pollen tube was found to have reached the nucellus region about 2 months later. There it makes contact with the enlarging gynospore, which is still in the stage of having only dividing peripheral nuclei and the huge central vacuole. Many observers have recorded that the pollen tube "splays" over the prothallus apex, but such an early contact as is here described does not appear to have been recorded before. The tube exerts pressure on the still thin gynospore membrane, causing a depression (Fig. 5), and continues its growth between the developing female prothallus and the nucellus tissue for a distance that may be as great as 1 mm. Sometimes two pollen tubes follow the same route, at other times they grow on different sides of the prothallus apex, compressing it (Fig. 6). In such a case when the prothallus tissue is developed a sharp beak may result. As the prothallus matures, its cells occasionally almost invest the pollen tube, though more usually there is only a shallow depression. The degree of "spread" of the pollen tube over the prothallus apex appears to be less than that recorded for other species in which contact would seem to be later.

Figure 7*a* shows the body cell after division of its nucleus, and Figure 7*b* the partial extrusion of the apparently equal-sized second male nucleus. A nucleus rather larger than the tube nuclei may be observed closer to the body cell. Elliot (1948) noted that the stalk nucleus adhered to the body cell in *Pherosphaera* to a late stage, and observed that this seemed to be a feature of most podocarps. Boyle and Doyle (1953) did not find such an association in *Podocarpus nivalis* but considered the matter worthy of further consideration.

(*b*) *Development of the Gynospore and Female Prothallus*

There is a single gynospore mother cell lying in a tapetal tissue which is clearly differentiated from the cells of the nucellus (Figs. 1, 2). This sporogenous group lies slightly below the junction of the nucellus beak with the integument.

The first division of the gynospore mother cell is shown in early telophase in Figure 8*a*. In the ovules collected on the same date (October 4, 1958) further stages in the development and enlargement of the sporogenous group were seen (Fig. 8*b*, *c*). The inner functional gynospore and its sister cell may have already been formed and enlarged before the micropylar cell has completed its division.



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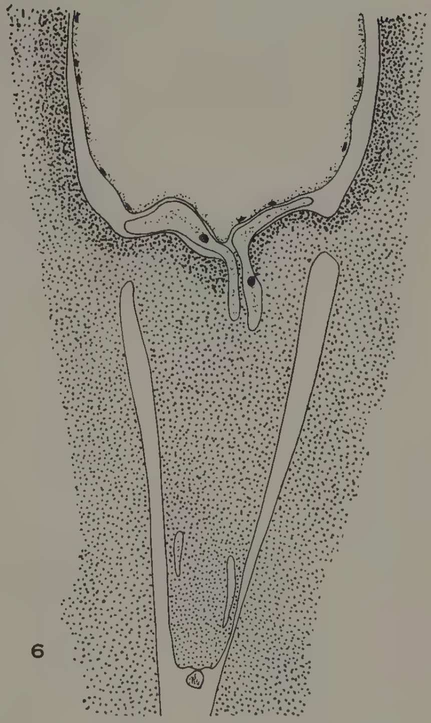

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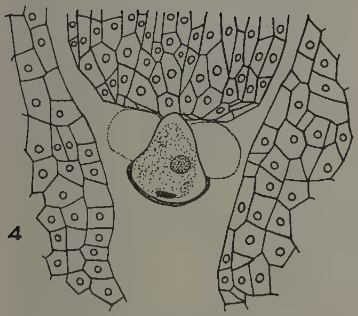

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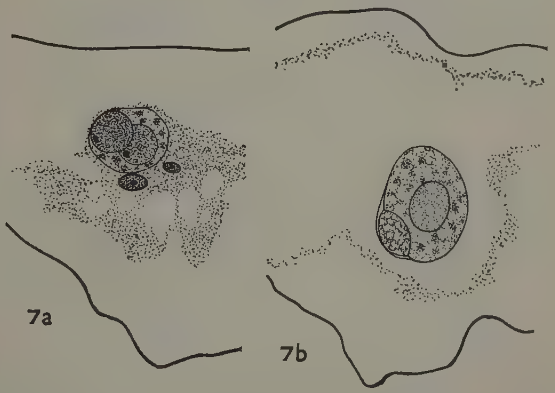

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Fig. 4.—Early stage in germination of pollen grain on nucellus beak. The use of the wings as flotation mechanisms on the inverted ovule is clear. 29.ix.1955. ×180. Fig. 5.—Pollen tube in contact with developing prothallus still in the free nuclear division stage and depressing it. 23.xi.1958. ×40. Fig. 6.—The two pollen tubes in contact with apex of developing female prothallus. 23.xi.1958. ×40. Fig. 7.—Development of male nuclei. In *a*, the two nuclei are still within the antheridial cell. Of the two nuclei lying free within the tube, the larger may be the stalk nucleus. 21.i.1955. In *b* is shown the partial extrusion of the second, non-functional male nucleus. 31.i.1958. ×90.

At this stage the uninucleate gynospore is somewhat smaller than the pollen grain as formed in the ripe anther. A linear tetrad of spores is shown in Figure 8*d*, the two at the micropylar end being appreciably smaller than the other pair. Enlargement of the functional gynospore, which lies at the chalazal end, proceeds rapidly (Fig. 8*e*). Figure 8*f* shows that by the same date its nucleus in some cases has already divided once.

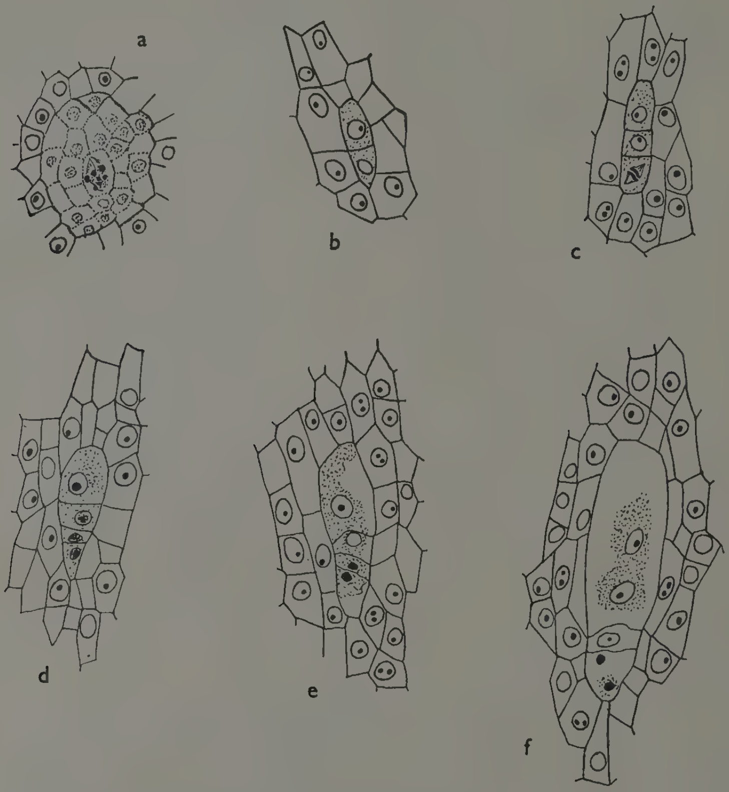
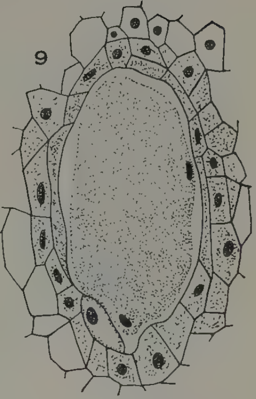


Fig. 8.—*a–f*, six stages in the development of the gynospore. *a–c*, 4.x.1958; *d*, 7.x.1958; *e*, *f*, 12.x.1958. All ×225.

During the next 3 weeks the usual enlargement of the spore, accompanied by free nuclear division, occurs with a peripheral distribution of the nuclei (Fig. 9). The tapetal and surrounding cells separate and disintegrate in the so-called spongy tissue. It will be noted, however, that at this stage there is no large central vacuole, but the cell is filled with a uniformly staining homogeneous material. This substance appears to be of a somewhat gelatinous consistency, for in some preparations it gives the appearance of having cracked or split on contact with the knife when in a dehydrated state. Developing prothalli with peripheral nuclei have been observed in this condition during a period of some 2 weeks, after which time the usual central vacuole appears.



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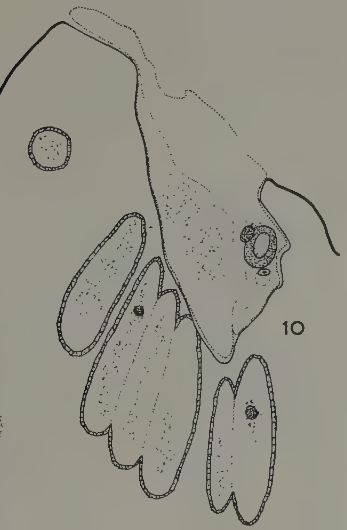

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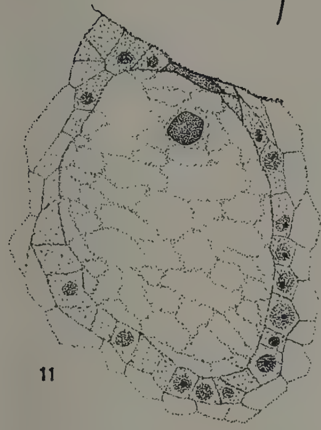

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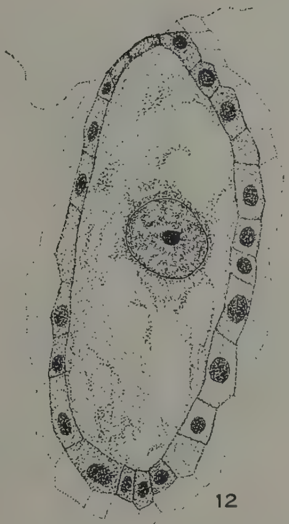

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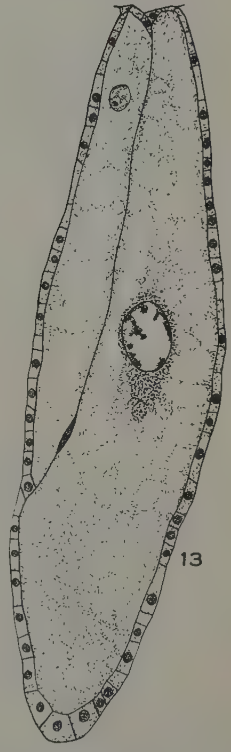

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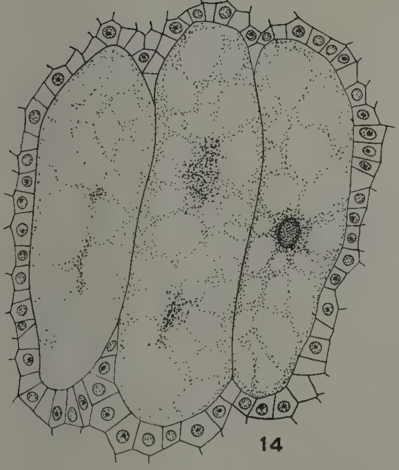

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Fig. 9.—Enlarging gynospore with free nuclear division. The vacuole is not yet developed but uniform dense contents are present. 2.xi.1958. ×180. Fig. 10.—Longitudinal section of prothallus apex, showing six archegonia in close association with pollen tubes. There are two of these, the outer of which shows the male cell, the non-functional male nucleus, and possible stalk cell. 23.i.1959. ×40. Fig. 11.—Longitudinal section of an immature archegonium, showing superficial neck cells. 23.i.1959. ×180. Fig. 12.—Longitudinal section of a single ripe archegonium. 23.i.1959. ×180. Fig. 13.—Longitudinal section of two archegonia of the long type. The two lie within one jacket. 31.i.1958. ×90. Fig. 14.—Transverse section of a prothallus, showing three adjacent archegonia lying within one jacket layer. 21.ii.1955. ×180.

Alveolar formation was first observed on January 3, 1959, 3 months after germination of the spore had begun. But, before alveoli are observed, the pollen tubes have grown the full length of the nucellar beak and begun to impinge on the gynospore membrane. They burrow between it and the integument, causing a depression of the membrane at the area of contact (Figs. 5, 6).

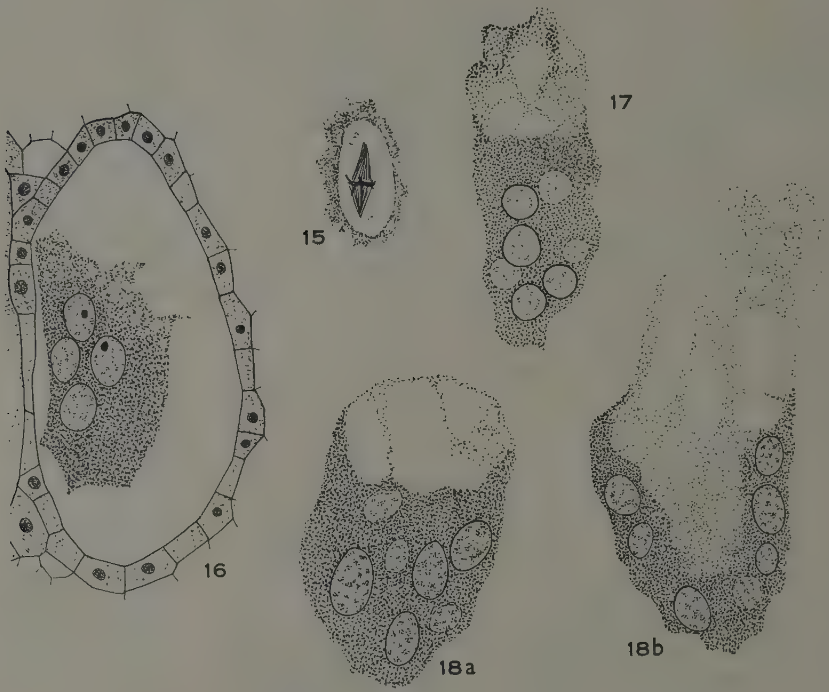


Fig. 15.—First division of the zygote nucleus. The spindle is intranuclear and along the long axis of the archegonium. 31.i.1958. ×180. Fig. 16.—Four nuclei resulting from the second division of the zygote. They are centrally placed in the archegonium. 23.i.1959. ×180. Fig. 17.—Eight-nucleate stage after the third division of the proembryo nuclei. They lie in dense protoplasm at the base of the archegonium. 31.i.1958. ×180. Fig. 18.—*a*, *b*, two consecutive sections of a late proembryo. 23.i.1959. ×180.

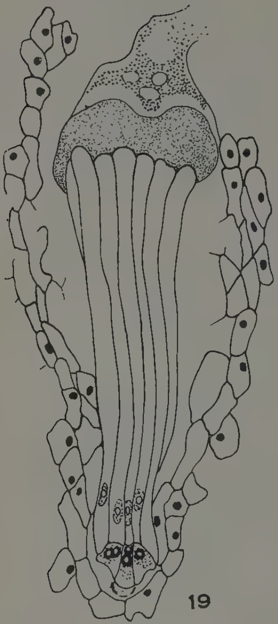
Several observers since the time of Coker (1902) have recorded that the pollen tubes in *Podocarpus* spp. "splay" over the apex of the female prothallus. Stiles (1912) in his Figure 28 certainly shows a lateral burrowing of the tube as well as the more generally recorded "spread". Boyle and Doyle (1953, Fig. 22) also show a "less common lateral burrowing". In *P. falcatus* such burrowing appears to be the normal procedure, and it occurs early before the prothallus tissue is developed. Nor is it possible to escape the conclusion that the presence of the pollen tube influences the development of the archegonia, which may be found in a row beneath the pollen tube (Fig. 10). Its presence also appears to inhibit the development of the outer and thicker gynospore membrane.

The phenomenon of a lateral burrowing by the pollen tube is well known in such diverse genera as *Sequoia* (Looby and Doyle 1942) and *Callitris* (Baird 1953), where the archegonia only develop along its course. It is not possible to be definite in all cases upon this point in *P. falcatus*. In older prothalli where archegonia of various ages may be found cut in different planes of section, it is quite possible that those isolated from the main group have been stimulated to develop by other pollen tubes not visible in that particular section and not clear in other sections of the same ovule. Certainly the shape of the prothallus apex after cell formation is markedly influenced by the pollen tubes which are not burrowing in the tissue. The prothallus has grown up around them.

The archegonia all appear to be superficial in origin (Figs. 11, 12). The presence of the pollen tubes prevents them from being occluded by upgrowth of the surrounding prothallus cells. They have a neck consisting of a single plate of some six to eight cells (Fig. 11). When isolated, each archegonium has a well-developed jacket layer, but several archegonia may be formed in close contiguity. Where this is so a single jacket invests the group, the individual archegonial protoplasts only being separated by their own walls (Fig. 14). The number of archegonia is variable; seven are shown in Figure 10 but as many as 12 have been counted in a single section. It appears that the shape of the archegonia varies from one season to another in prothalli collected from the same tree. Thus Figure 13 shows a long archegonium (730 μ), typical of those collected in 1958; but the following year they were shorter and blunter, varying from 160 to 220 μ in length. In the young archegonium the nucleus lies below the neck cells; but, after the division giving the ventral canal nucleus and egg, the latter moves to a more central position, enlarges, and becomes intested by denser cytoplasm. The ventral canal nucleus does not persist for long.

(*c*) *Proembryo*

The fusion of egg and male nucleus has not been observed. In material fixed on January 31, 1958, the first division of the zygote nucleus was found placed centrally in the archegonium (Fig. 15). The spindle is intranuclear, and its axis is roughly aligned along the major axis of the archegonium. One further division occurs in the mid archegonial region; Figure 16 shows the four resulting nuclei within the dense protoplasmic mass that surrounds the egg. The four nuclei then migrate to the base of the archegonium, where they are embedded in dense, non-vacuolate protoplasm. Figure 17 shows seven of the eight nuclei that result from the third division. Two further free nuclear divisions occur. Figures 18*a* and 18*b* are drawn from two consecutive sections. Portions of this particular proembryo occurred in seven sections of 10 μ thickness. I was unable accurately to determine the number of nuclei involved, for it is possible for a particular nucleus to occur in more than one section. It may be of the order of 32 but possibly only 16, i.e. the result of the fourth and not the fifth free division. That five free divisions do occur is obvious from the high number (25) of cells observed where the suspensor is cut in transverse section when it is coiled spirally within the archegonial cavity.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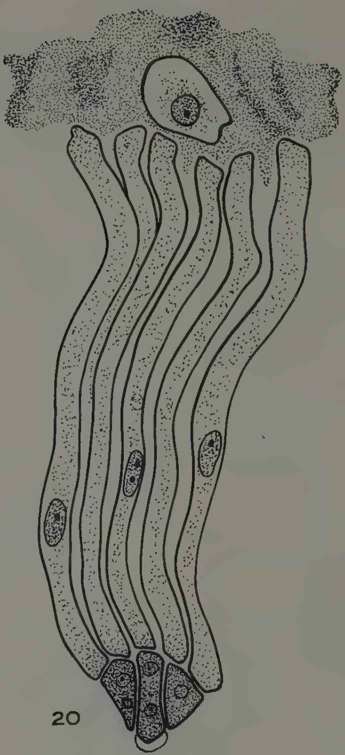
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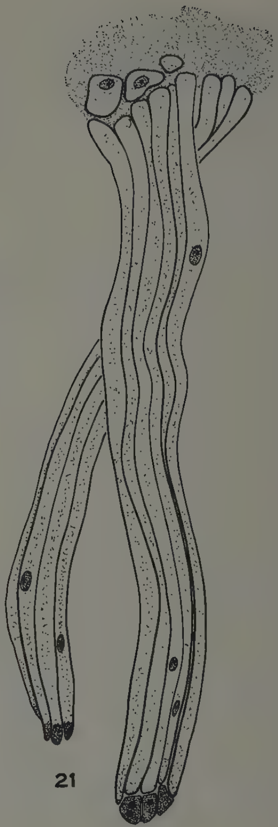
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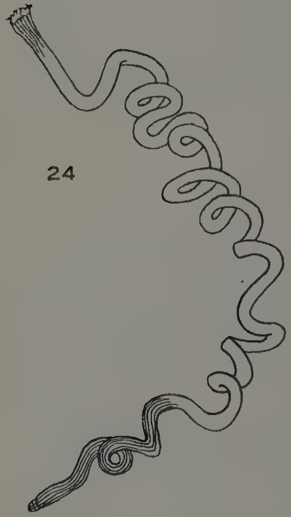
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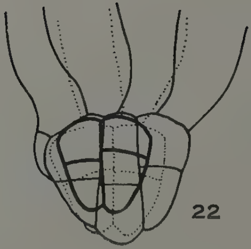
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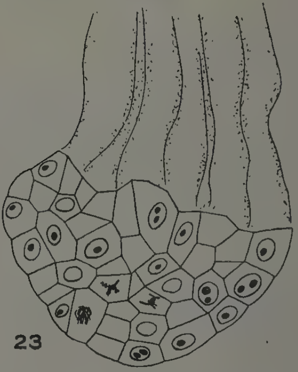
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Fig. 19.—Developing embryo, showing binucleate embryonic cells, one of which shows a "cap". There is a well-developed plug at the archegonial end of the suspensor, above it three degenerating nuclei. 5.ii.1959. ×90. Fig. 20.—Developing embryo with three binucleate embryonic cells, one of which has a cap. Above the suspensor is a degenerating cell, probably of the upper tier. 13.ii.1959. ×180. Fig. 21.—Simple polyembryony. The stronger embryo shows binucleate cells in the embryonic group. Above the plug are degenerating cells of the upper tier. 19.ii.1959. ×90. Fig. 22.—Embryo, showing four tetrads. 25.ii.1959. ×180. Fig. 23.—Embryo. 23.iii. 1955. ×180. Fig. 24.—Embryo from a dissection. Apr. 1959. Freehand, c. ×4.

(*d*) *Embryo*

It has not been possible to follow the rearrangement of the proembryonic nuclei into the tiered state. The preparations made show only oblique sections, probably because of the somewhat haphazard placing of the archegonia in the prothallus. It is clear from those sections in which the upper tier, the suspensor tier, and the embryonic cells can be recognized that there is a number of relict nuclei which do not enter into the constitution of these layers. That a sixth, internal division does occur is clear from the binucleate state of the embryonic cells when the suspensor cells have begun to elongate. The number of embryonic cells is variable—three to five, arranged in a single layer. In Figures 19 and 20 the elongating suspensor cells have pushed the embryonic cells into the prothallus "cone". In each case only one of the cells in the layer shows a developing "cap". These suspensor cells show clearly the "plug" at the archegonial end with nuclei either embedded in it or in an obviously unhealthy state above it. Figure 21 shows a case of simple polyembryony in which the two fertilized archegonia must have been very close together. At this stage the basal part of the suspensor cells, that adjacent to the embryonic layer, has much starch, which is also found in the surrounding cells of the cone tissue but not elsewhere in the prothallus.

The two nuclei of the binucleate cells divide simultaneously, leading to the formation of tetrads (Fig. 22). A later stage of embryo formation is seen in Figure 23, which shows a dome-shaped mass of cells with embryonic tubes, or secondary suspensor, above it. It is obvious that a unity of growth and development must have been established among the embryonic cells, although, to judge from the constitution of younger embryos, there is every reason to conclude that more than one tetrad was involved in its structure.

As the suspensor elongates, pushing the embryo into the cone tissue, it is thrown into corkscrew-like folds, particularly within the archegonial cavity. Where such folds are cut transversely it is easy to count the number of cells involved. The numbers varied from 9 (occurring twice) to 25 (also twice). The majority of the counts were 23 and 24. From this it is legitimate to assume that five free mitoses have taken place in the proembryo stage. In the case of the two very low numbers (9), is it possible that the fifth free division was omitted?

In the elongation of the suspensor it is not unusual for some of the cells to peel off at an early stage. In such cases a small amount of terminal proliferation occurs in the archegonial cavity. Some preparations show a tangled mass of suspensor cells showing proliferation, all confined within the archegonial cavity. It would appear that, in these cases, the embryo is in process of abortion, being unable to escape from the archegonium.

True fission polyembryony does not seem to be common in *P. falcatus*, the majority of embryos dissected out being of the type shown in Figure 24. In such cases this suspensor is about 2 cm long when the spiral is fully extended but not straightened out.

In the ripe seed the embryo is 3·5–4·0 mm long. The growing apex lies between two rudimentary cotyledons only 0·75–1·0 mm in length. The endosperm contains oil and but little starch.

IV. DISCUSSION

In 1954 Doyle, having completed a very full account of the gametophyte and embryogeny of *Podocarpus nivalis* (Boyle and Doyle 1953, 1954), discussed the basal embryogeny and evolutionary tendencies of the Podocarpaceae. He concluded that in the family as a whole there was: (i) a shortening of the life cycle from 2 years to 1 year by dropping the rest period following pollination; (ii) a reduction of one of the male cells to a nucleus extruded from the antheridium; (iii) an increase in the number of male prothallial cells with a subsequent increase in the number of free nuclei in the pollen tube; (iv) the development of shorter, blunter archegonia, replacing the long narrow type; (v) an increase in the number of archegonia; (vi) a tendency for the archegonia to be deeply embedded in the lower stachycarps and to have grossly unequal gamete nuclei.

In the same (1954) paper Doyle tabulated the distribution of primitive and advanced features in the podocarps as a whole. He considered that the higher members of the subgenus *Stachycarpus* showed, or might be expected to show, the following features: (i) a life cycle of the 2-year type; (ii) a low number, up to three, of separate archegonia, possibly embedded; (iii) five free mitoses in the early embryogeny, two occurring in the mid archegonial region; many embryonic cells in one tier.

It is not the purpose of the present paper to discuss the podocarp life cycle as a whole, but to record certain features in *P. falcatus* that are more advanced than was expected even in a higher member of *Stachycarpus*. These are that the life cycle is of the 1-year type with no halt after pollination, and that the superficial archegonia are many and at times grouped within a common jacket layer. Though only of intermediate length, archegonia of a narrow type do occur, together with others that are blunt-ended. The primitive proembryo stages of five simultaneous divisions, two in mid archegonial regions, do occur. On the other hand the embryonic cells are few and arranged in one tier.

The early contact between pollen tube and the developing female prothallus, with continued growth of the tube between gynospore membrane and nucellus, does not appear to have been recorded before. Although the penetration of the tube is not as deep as in *Sequoia* or *Callitris*, its presence does seem to influence the development of the archegonia along the line of contact.

Doyle treated the subgenus *Stachycarpus* as a unit. Buchholz and Gray (1948) divided it into several sections on the basis of leaf anatomy. It may be thought that the points of difference mentioned above lend support to the view that *P. falcatus* may conveniently be placed in the section *Afrocarpus*.

V. ACKNOWLEDGMENTS

I am greatly indebted to the late Professor J. G. Wood of the Department of Botany, University of Adelaide, for the facilities that were placed at my disposal in his laboratory.

My thanks are also due to Mr. T. R. N. Lothian, Director of the Adelaide Botanic Garden, for permission to collect material there. The majority of the figures were drawn by Mrs. H. W. Woolhouse, to whom I am very grateful.

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STUDIES ON THE ORIGIN, EVOLUTION, AND DISTRIBUTION OF THE GRAMINEAE

III. THE TRIBES OF THE SUBFAMILY ERAGROSTOIDEAE

By W. Hartley* and Christine Slater*

[*Manuscript received March* 7, 1960]

Summary

In further studies of grass distribution, maps are presented showing the world distribution of the Eragrosteae (*sensu str.*) and of the subfamily Eragrostoideae within which it is included. Both taxa show centres of high relative specific differentiation in inland Australia and in South West Africa, but in addition, the subfamily has centres of differentiation in the Sahara region, northern Mexico, and north-western India.

The centres of differentiation are all in regions of hot, arid climate near the tropics of Cancer and Capricorn. The close relationship between climate and distribution is most apparent in the case of the subfamily Eragrostoideae, species of which are relatively abundant in the grass flora of all arid regions with high winter temperatures and summer or non-seasonal rainfall incidence.

The distributions of most of the other tribes and subtribes which have been included in the Eragrostoideae show a similar relationship to climate. Some apparent exceptions to this are discussed, and it is shown that the geographical evidence supports conclusions from recent cytotaxonomic and anatomical studies that the taxa concerned should be removed from the subfamily.

The very wide distribution of the subfamily and of its constituent taxa, as well as the close relationship between the distribution pattern and climate, suggests that the subfamily is a very old one. Geographical and taxonomic evidence indicates that it may have originated in tropical or subtropical Africa at least as early as the Oligocene.

I. Introduction

The present paper continues studies of the distribution of the principal tribes of the Gramineae, with special reference to the effect of climatic and historical factors. The paper deals with the tribe Eragrosteae and those tribes and subtribes which are closely related to it. As in previous studies (Hartley 1958*a*, 1958*b*), the distribution has been shown by mapping the percentage frequency of species of the taxon concerned, in comparison with the total number of grass species occurring in each region. This method has proved useful for mapping distribution on a broad global basis, but is not suited for the study of local distribution.

II. The Tribe Eragrosteae and its Affinities

The modern concept of the tribe Eragrosteae is chiefly due to Hubbard (1934), following Stapf (1898). These authors brought together as a separate tribe a number of genera most of which had previously been included in the Festuceae and Chlorideae

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but which were distinguished by several morphological and anatomical characters, including the one- to three-nerved lemmas and a characteristic type of leaf structure.

Recent authors have generally accepted the taxon as a natural one, but there have been marked differences of viewpoint regarding its status and its relationship to other taxa. The most comprehensive treatment is that of Pilger (1954*a*, 1956), who grouped the genera placed in Eragrosteae by Hubbard as the subtribe Eragrostinae in a broader tribe Eragrosteae, which in turn formed part of the subfamily Eragrostoideae. Pilger's classification of this subfamily is shown in Table 1.

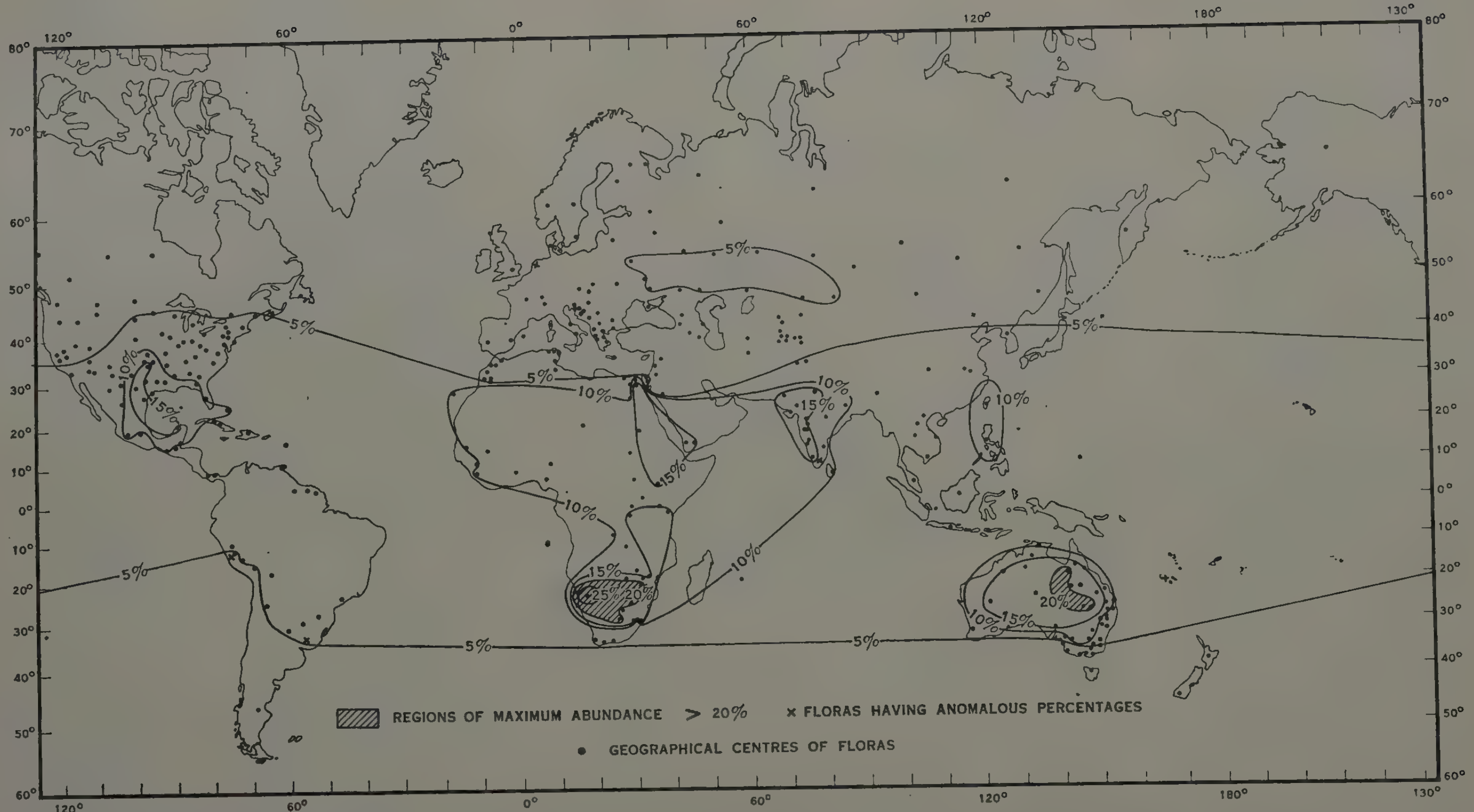
TABLE 1

CLASSIFICATION OF THE SUBFAMILY ERAGROSTOIDEAE PILGER

Tribe	Subtribe	Approx. No. of:	
		Genera	Species
Eragrosteae Benth.	Eragrostinae Ohwi	40	469+
	Scleropogoninae Pilger	1	1
	Lycurinae Pilger	2	5+
	Garnotiinae Pilger	1	30
	Sporobolinae Ohwi	7	174
	Muhlenbergiinae Pilger	1	100
Phaenospermeae Roshev.		1	1
Chlorideae Kunth	Lepturinae Hansen & Potztal	2	9+
	Chloridinae Pilger	32	186+
Aristideae Hubbard & Vaughan		3	308+
Lappagineae Link		15	45+
Jouveeae Pilger		1	2

Some significant changes in this grouping are proposed by authors who have investigated the morphology, anatomy, and cytology of the grasses concerned. Thus several recent American authors (Stebbins 1956; Reeder 1957; Brown and Emery 1958) follow Prat (1936) in including the tribe Pappophoreae Kunth in the same subfamily as the Eragrosteae. This view is also adopted by the Japanese botanists Ohwi (1942) and Tateoka (1957*a*). The latter also includes the tribe Spartineae C. E. Hubbard in the Eragrostoideae, but removes from the subfamily the subtribe Garnotiinae (tribe Garnotieae Tateoka) and the tribes Phaenospermeae and Aristideae.

Because of the conflicting views on broad taxonomic relationships, the discussion of geographical distribution which follows deals firstly with the Eragrosteae subtribe Eragrostinae Ohwi. This is followed by a discussion of the distribution of the subfamily Eragrostoideae as recognized by Pilger, modified to some extent by the views of other taxonomists.


5%
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REGIONS OF MAXIMUM ABUNDANCE > 20%
× FLORAS HAVING ANOMALOUS PERCENTAGES
● GEOGRAPHICAL CENTRES OF FLORAS
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60°
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120°
180°
130°
80°
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30°
20°
10°
0°
10°
20°
30°
40°
50°
60°

Fig. 1.—Map of world distribution of the Eragrosteae Benth. subtribe Eragrostinae Ohwi. Distribution expressed as percentage of species of Eragrostinae in the total grass flora.

III. Distribution of the Subtribe Eragrostinae Ohwi

The distribution of this subtribe, prepared on a percentage frequency basis similar to that used in mapping the Andropogoneae and Paniceae (Hartley 1958*a*, 1958*b*) is shown in Figure 1. The limits of the subtribe as given by Pilger (1954*a*, 1956) have been adopted in preparing this map, although Pilger excludes from it several genera, notably the rather large Australian genera *Plectrachne* and *Triodia*, which have been placed in the Eragrosteae by Hubbard and other taxonomists. Conversely, he includes in the subtribe the small genera *Monroa* and *Blepharidachne* which are considered by other authorities to have different affinities.

The distribution pattern as shown on the map is much less clearly defined than was the case for the Andropogoneae and Paniceae. There is no single zone of highest concentration, the lines of equal percentage frequency show marked irregularities, and there are several isolated pockets of apparently anomalous high or low values. The main features of interest shown by the map are:

(1) The zones of relatively high frequency occur on or near the tropics of Capricorn and Cancer.
(2) Correspondingly low percentage frequencies occur in the equatorial zone and at high latitudes.
(3) The regions of high percentage frequency have hot, arid climates (e.g. central Australia and South West Africa).
(4) The subtribe is relatively more abundant in southern than in northern latitudes, and in the eastern than in the western hemisphere.

The localities with the highest percentages of species of the subtribe, all of which are in Australia or Africa, are given in Table 2.

Some of the irregularities and apparent anomalies of the distribution pattern shown on the map (Fig. 1) are a direct consequence of the small size of the taxon. The subtribe Eragrostinae as circumscribed by Pilger includes only about 470 species. This contrasts with the 850 species of the tribe Andropogoneae and more than 1460 species of Paniceae. In mapping the Eragrostinae, frequency lines have been shown at 5 per cent. intervals instead of the 10 per cent. intervals used for the Andropogoneae and the Paniceae. With such relatively small intervals the inclusion or omission of a single species, reflecting perhaps local climatic or edaphic conditions or possible errors in the records, may result in major changes in the distribution pattern. This could largely account for the size and shape of the 5–10 per cent. zone shown in southern Russia, and also for some of the minor anomalies elsewhere.

There remain, however, certain anomalies in the distribution pattern which cannot readily be attributed to the techniques of mapping. This is true of the relationship between distribution and climate. The high percentage frequency of species in South West Africa and central Australia is in accordance with the generally accepted view that the Eragrostinae occur predominantly in regions of hot, dry climate. A similar general relationship with climate is also evident in the northern and western hemispheres, but the percentage frequencies in these regions never exceed 20 per cent. From climatic considerations, very high percentage frequencies might be expected in the hot arid regions of the south-western United States and northern Mexico, but in fact the highest values recorded are much below those generally found in southern Africa and central Australia.

It appears, therefore, that the view previously expressed (Hartley 1950), that there is little indication of the effect of historical factors in the present distribution of the Eragrostinae, requires some modification in the light of the more detailed study now made. While it remains true that the Eragrostinae are relatively most abundant in regions of high winter temperature and low rainfall, the influence of temperature being more important than that of moisture, the differences between overall frequency levels in different hemispheres suggest that the distribution has been influenced by factors other than climatic ones.

Table 2

REGIONS WITH HIGHEST PERCENTAGES OF SPECIES OF ERAGROSTINAE

Region	No. of Grass Spp.		Per Cent. of Eragrost.	Reference
	Total	Eragrost.		
South West Africa	203	52	25·6	Pilger 1954*b*
Queensland: Maranoa district	150	33	22·0	Queensland Herb.
Queensland: Warrego district	146	31	21·3	Queensland Herb.
Queensland: Bourke district	234	47	21·0	Queensland Herb.
Bloemfontein and Brandford, O.F.S., South Africa	139	29	20·9	Mostert 1958
Transvaal, South Africa	251	52	20·7	Stent 1924
Southern Rhodesia: Southern Division	171	35	20·5	Sturgeon 1953–1955
Tibesti, Sahara	95	19	20·0	Quezel 1958
Southern Rhodesia: Western Division	196	39	19·9	Sturgeon 1953–1955
Central Australia	138	27	19·6	Chippendale 1959

Among the factors which might be expected to affect the relationship between distribution and climate would be the evolutionary history of the taxon. If the subtribe Eragrostinae had originated in the southern parts of the eastern hemisphere, in a relatively recent geological period, it might not have had time to spread fully and reach a balanced distribution in the northern and western hemispheres. Such a recent origin would be reflected in the taxonomy of the subtribe at the generic and infra-generic levels.

The subtribe Eragrostinae includes 40 genera (Pilger 1956). *Eragrostis*, with 300 species, is by far the largest genus; four others have each more than 12 species; while no less than 18 genera are monospecific. It is a striking fact that with one exception all the genera and subgeneric taxa with more than 10 species are very widely distributed, occurring in both the eastern and western hemispheres and north and south of the equator. Such larger taxa include the genera *Tripogon*, *Diplachne*, and *Leptochloa*, as well as the sections *Cataclastos*, *Eragrostis*, and *Platystachya* of the large genus *Eragrostis*. The single exception is the genus *Tridens*, with about 15 species in North and South America. Each monospecific genus naturally has a restricted distribution, but some of these occur in the western hemisphere, and others in the northern and southern parts of the eastern hemisphere.

This distribution pattern does not support the view that the subtribe is of recent origin, but rather that it has had a long evolutionary history, in the course of which it has been able to spread to all parts of the world.

The apparent anomalies in the relationship between distribution and climate may, however, be due to differential competition, in various parts of the world, between species of the subtribe and those of related taxa with a similar climatic response. It is therefore important to consider the distribution of the other taxa of the tribe Eragrosteae (*sensu lat.*) and of the subfamily Eragrostoideae, within which the tribe is included.

IV. Distribution of Taxa related to the Eragrostinae

Because of the relatively small size of many of the taxa which have been considered by Pilger and others to be closely related to the Eragrostinae, it is impracticable to map their distribution in detail. Even in the larger taxa, with 100 to 300 species, the reliability of the mapping would be greatly reduced by minor errors in the available data.

It is, however, possible to compare geographical distribution by listing, for each of the tribes and subtribes concerned, the localities in which they occur with greatest relative frequency. It is then possible to determine how far these localities coincide for different taxa. Since the total number of localities for which floristic data have been examined exceeds 400, and these are very widely scattered throughout the world, it is evident that such coincidences within the 10 highest recorded values for each of the taxa concerned will rarely occur fortuitously.

Table 3 shows the 10 localities with the highest recorded percentage frequencies of species of each of the following taxa:

Eragrosteae Benth. subtribe Eragrostinae Ohwi,
Eragrosteae Benth. subtribe Sporobolinae Ohwi,
Eragrosteae Benth. subtribe Muhlenbergiinae Pilger,
Chlorideae Kunth subtribe Chloridinae Pilger,
Aristideae Hubbard & Vaughan,
Lappagineae Link,
Pappophoreae Kunth.

The tribes and subtribes listed above include all those with more than 30 species which are included in the subfamily Eragrostoideae in the classification adopted by Pilger (Table 1) as well as the Pappophoreae, which other authors include in this subfamily.

TABLE 3

REGIONS WITH THE 10 HIGHEST PERCENTAGE FREQUENCIES OF SPECIES OF THE LARGER TRIBES AND SUBTRIBES OF THE SUBFAMILY ERAGROSTOIDEAE

Region	Ten Highest % Frequencies of Spp. of:							Ref.*
	Subtribes				Tribes			
	Eragrostinae	Sporobolinae	Muhlenbergiinae	Chloridinae	Aristideae	Lappagineae	Pappophoreae	
AFRICA								
Egypt: Isthmic Desert					×			(1)
Egypt: Sinai					×			(1)
Oases of Libyan Desert					×			(1)
Tibesti, Sahara	×				×		×	(2)
Sagan-Omo, Ethiopia		×						(3)
Western British Somaliland		×		×		×		(4)
North-eastern Kenya				×				(5)
South-eastern Kenya		×						(5)
Katanga, Belgian Congo		×						(6)
Western Southern Rhodesia	×				×			(7)
Southern Southern Rhodesia	×							(7)
Transvaal	×							(8)
Bloemfontein and Brandford, O.F.S.	×							(9)
Mauritius		×						(10)
South West Africa	×	×			×	×		(11)
ASIA								
North-western Arabia					×			(12)
South-western Arabia						×		(12)
Bombay: Sind region		×						(13)
Bombay: Gujarat region						×		(13)
Agra district, India						×		(14)
Lesser Sunda Islands						×		(15)
AUSTRALIA								
Western Australia: Northern							×	(16)
Western Australia: Eremaean							×	(16)
Central Australia	×						×	(17)
Northern South Australia							×	(18)
Queensland: Gregory North							×	(19)
Queensland: Bourke	×						×	(19)
Queensland: Mitchell					×		×	(19)
Queensland: Maranoa	×						×	(19)
Queensland: Leichhardt							×	(19)
Queensland: Warrego	×							(19)
New South Wales, SE. Riverina						×		(20)

TABLE 3 (*Continued*)

Region	Ten Highest % Frequencies of Spp. of:							Ref.*
	Subtribes				Tribes			
	Eragrostinae	Sporobolinae	Muhlenberginae	Chloridinae	Aristideae	Lappagineae	Pappophoreae	
AMERICA								
Nebraska, U.S.A.			×					(21)
Kansas, U.S.A.			×					(21)
Arizona, U.S.A.			×					(21)
Grand Canyon, Arizona			×					(22)
New Mexico, U.S.A.			×					(21)
Jornada Exp. Range, New Mexico		×	×	×	×			(23)
Texas: Edwards Plateau				×				(24)
Texas: Trans-Pecos area			×	×	×			(24)
Texas: Plains country				×				(24)
North-western Sonora, Mexico			×	×		×		(25)
Coahuila, Mexico			×	×				(26)
Michoacan, Mexico						×		(27)
Mexico City, Mexico		×	×					(28)
Yucatan, Mexico				×				(29)
Bahamas		×						(30)
Santa Fe, Argentina				×				(31)
Peru: Lima district						×		(32)

* References: (1) Tackholm and Drar 1950. (2) Quezel 1958. (3) Chiovenda 1951. (4) Hubbard 1941. (5) Bogdan 1958. (6) De Wildeman 1921. (7) Sturgeon 1953–1955. (8) Stent 1924. (9) Mostert 1958. (10) Hubbard and Vaughan 1940. (11) Pilger 1954*b*. (12) Blatter 1936. (13) Blatter and McCann 1935. (14) Bharadwaja, Chaudhary, and Sinha 1956. (15) Kalkman 1955. (16) Gardner 1952. (17) Chippendale 1959. (18) Black 1943. (19) Queensland Herbarium (unpublished data). (20) Moore 1953. (21) Hitchcock 1935. (22) Bailey 1957. (23) Little and Campbell 1943. (24) Cory and Parks 1937. (25) White 1948. (26) Johnston 1943. (27) Leavenworth 1946. (28) Reiche 1923. (29) Standley 1930. (30) Hitchcock 1936. (31) Ragonese 1941. (32) Macbride 1936.

In each of the columns headed by the name of a tribe or subtribe there are 10 crosses, corresponding with the 10 localities (indicated in the left-hand column) with the highest percentage frequencies of species of the tribe concerned in all the floras which have been examined. Thus the highest percentage frequencies of species of the subtribe Eragrostinae occur in Tibesti, western and southern Southern Rhodesia, Transvaal, Orange Free State, South West Africa, central Australia, and three of the pastoral districts of Queensland, as shown also in Table 2. For convenience, the localities have been grouped together in the continents.

It is evident from the table that high values for some of the taxa occur predominantly in particular continents. Thus the 10 highest percentages of the subtribe Muhlenbergiinae are all in the United States and Mexico, while nine of the 10 highest percentages of the Pappophoreae are in Australia. On the other hand, the tribes Aristideae and Lappagineae, and the subtribe Sporobolinae, show less evidence of geographical concentration, high values being recorded for three or four of the continents. None of the high values for any of the taxa are found in Europe. Certain localities have a grass flora with high percentages of species of three or four of the seven taxa recorded. These localities are Tibesti (Sahara), Western British Somaliland, South West Africa, the Jornada Experimental Range in New Mexico, the Trans-Pecos region of Texas, and north-eastern Sonora in Mexico.

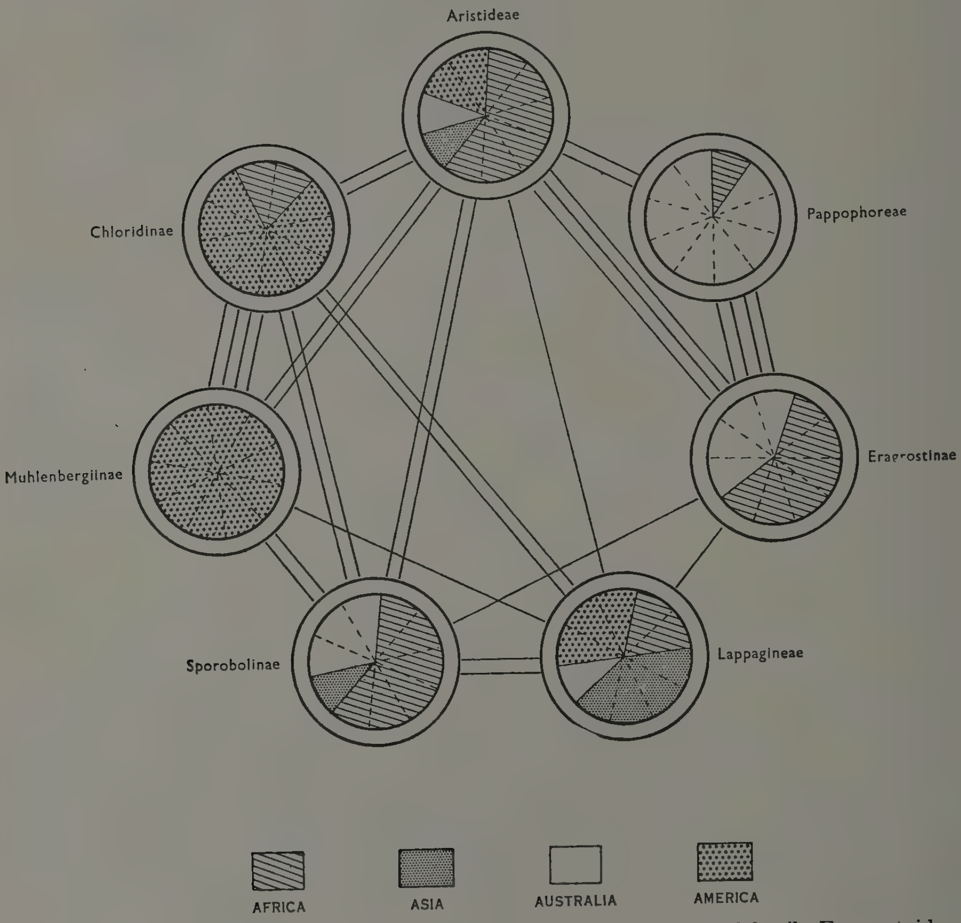

Fig. 2.—Geographical affinities of the larger tribes and subtribes of the subfamily Eragrostoideae (based on data from Table 3). For explanation see text.

The data from Table 3 are shown diagrammatically in Figure 2, which indicates more effectively the geographical relationships of the taxa concerned. The size of the sectors within each circle indicates the number of localities with the 10 highest recorded percentages of the tribe or subtribe concerned in each continent. Thus, of the 10 localities with the highest percentages of species of Aristideae, six are in Africa, two in America, and one each in Asia and Australia. The number of lines joining the circles representing each two taxa indicates the number of localities in which both are present in high frequency. Thus, of the 10 localities with the highest percentages of species of Chloridinae, two are also among the 10 localities with the highest percentages of species of Lappagineae. Where there is no line connecting two taxa, this indicates that among the 10 localities of highest percentage in each case, there are none in common.

Figure 2 shows the close geographical relationship in the distribution of the seven tribes and subtribes. In some instances this relationship is direct, as when three or four localities have high percentage frequencies of species of each of two tribes. The Chloridinae and the Muhlenbergiinae are closely linked in this way, as are the Pappophoreae and the Eragrostinae. In other instances the geographical relationship is indirect. Thus there is no direct linkage between the Pappophoreae and the Muhlenbergiinae, which occur predominantly in different continents, but the two taxa are nevertheless linked through the Aristideae and Chloridinae. The degree of geographical linkage between any two taxa is not necessarily evidence of a corresponding degree of taxonomic relationship, but, taken as a whole, the closely reticulated system of geographical relationships suggests that the tribes and subtribes have close taxonomic affinities. By contrast, there are no corresponding geographical relationships between the tribes Andropogoneae and Paniceae which have been previously studied (Hartley 1958*a*, 1958*b*); nor, with one minor exception, is there any geographical linkage between either of these tribes and the taxa of the subfamily Eragrostoideae.

Because of the small numbers of species involved, it is not possible to show in a similar way the geographical relationships of the remaining taxa of the subfamily Eragrostoideae. However, the subtribes Scleropogoninae and Lycurinae of the Eragrosteae, and the tribe Jouveeae, all have a concentration in the southern United States and Mexico, similar to that of the Muhlenbergiinae and the Chloridinae. The subtribe Lepturinae of the Chlorideae is widely distributed from east Africa to Australia and Polynesia, with perhaps its main concentration in Queensland; a distribution which fits in fairly well with that of the subfamily as a whole, although it is quite distinct from that of the subtribe Chloridinae, to which it is most closely allied in Pilger's classification.

On the other hand, the subtribe Garnotiinae of the Eragrosteae, and the tribe Phaenospermeae, appear to lie quite outside the pattern of geographical relationships which is apparent in the other taxa of the subfamily Eragrostoideae.

The Garnotiinae consist of a single genus, *Garnotia*, with about 30 species mainly in Indo-Malaysia and Polynesia, while the Phaenospermeae is a monospecific tribe indigenous to central and southern China (Pilger 1956). The status and relationships of these taxa have long been in doubt, and few authors agree with Pilger in placing them in the Eragrostoideae. *Garnotia* has been placed by various authorities

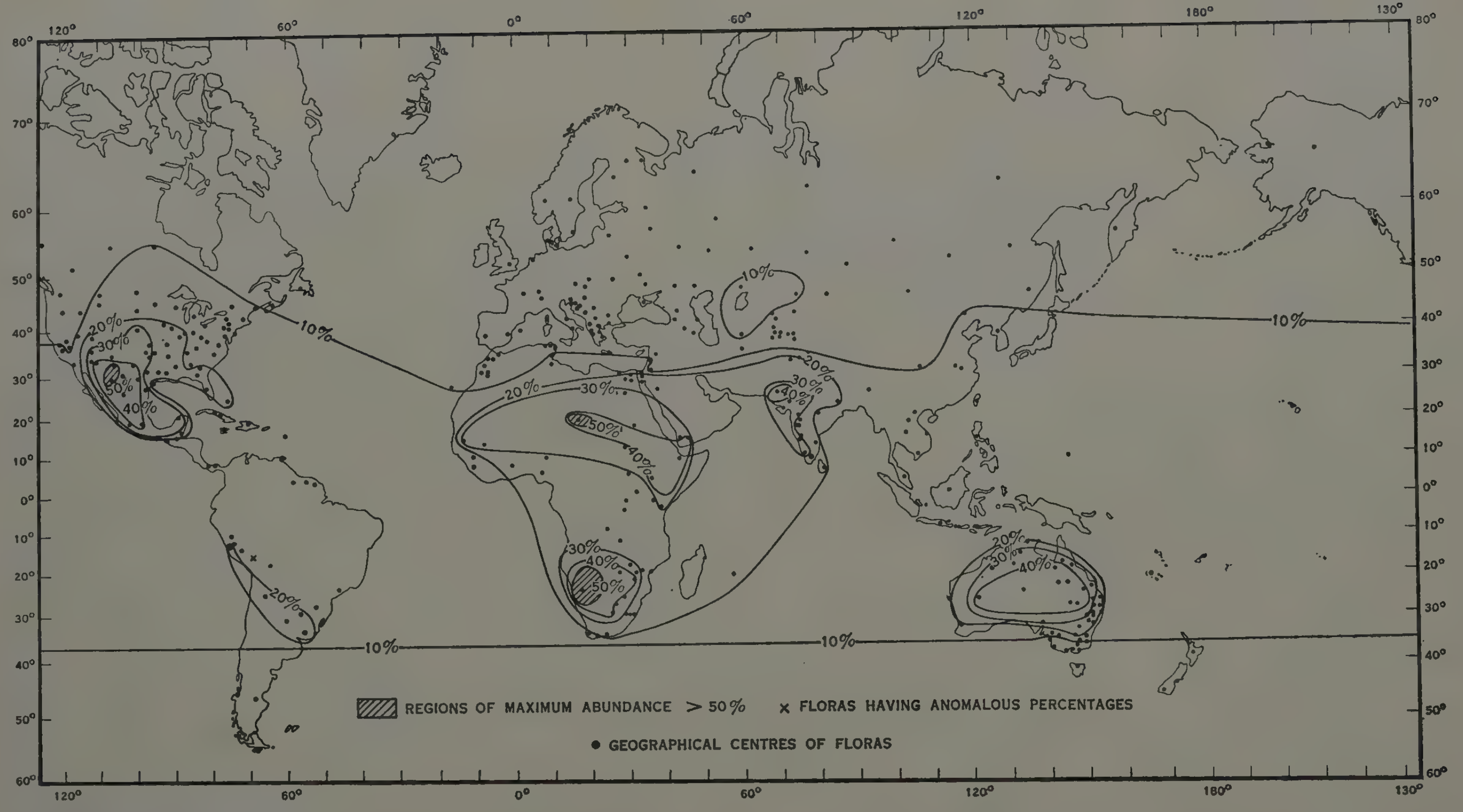
REGIONS OF MAXIMUM ABUNDANCE > 50%
× FLORAS HAVING ANOMALOUS PERCENTAGES
● GEOGRAPHICAL CENTRES OF FLORAS
10%
20%
30%
40%
50%
120°
60°
0°
60°
120°
180°
130°
80°
70°
60°
50°
40°
30°
20°
10°
0°
10°
20°
30°
40°
50°
60°

Fig. 3.—Map of world distribution of the subfamily Eragrostoideae Pilger. Distribution expressed as percentage of species of Eragrostoideae in the total grass flora.

in such distantly related tribes as Paniceae, Tristegineae, Arundinelleae, and Agrostideae (Santos 1944). Consideration of cytological and anatomical data led Tateoka (1957*a*) to conclude that: "*Garnotia* should be separated from Eragrosteae, and may be treated as an independent tribe, Garnotieae, which has relationship with Arundinelleae".

Similarly, this author follows Ohwi (1942) and Rozhevits (1945) in placing the Phaenospermeae with the Arundoideae or Phragmitiformes rather than with the Eragrostoideae. Recently, after reviewing all the evidence, including particularly the morphology and leaf anatomy, Conert (1959*a*) has concluded that *Phaenosperma* is related to the Stipeae rather than the Eragrostoideae.

If these two taxa are considered to fall outside the proper limits of the Eragrostoideae, the remainder of the subfamily shows a remarkably coherent pattern of geographical relationships. The distribution of the subfamily, as so limited, is discussed below, as well as the relationship of this distribution to climatic factors.

V. DISTRIBUTION OF THE SUBFAMILY ERAGROSTOIDEAE

The distribution of the subfamily Eragrostoideae as delimited by Pilger, but excluding the Garnotiinae and Phaenospermeae and including the Pappophoreae, is shown in Figure 3.

The map resembles the distribution map of the Eragrostinae (Fig. 1), but the frequency zones are generally more clearly defined, with fewer irregularities and apparent anomalies. This clearer definition is partly due to the fact that the lines correspond with 10 per cent. frequency intervals instead of the 5 per cent. intervals used in Figure 1.

There is a shift in the zones of high concentration towards the western and northern hemispheres. In three regions—South West Africa, the Tibesti region of the Sahara, and a belt from south-western New Mexico to north-eastern Sonora—more than half of all the grasses are species of Eragrostoideae. High concentrations also occur in regions adjacent to these, as well as in the interior of Australia, the arid parts of West Pakistan, and parts of north-eastern Africa from northern Kenya to Somaliland (Table 4). Relatively low percentage frequencies are general in the equatorial belt and also, with the partial exception of central North America, in latitudes above 40°.

All the high concentrations of species of Eragrostoideae occur in arid regions, as may be noted by comparing Figure 3 with the UNESCO map of arid homoclimates (Meigs 1953). However, aridity alone does not determine the distribution of the subfamily, other factors of importance being temperature and the seasonal distribution of the rainfall. This is evident from Figure 4, in which symbols showing localities with percentages of species of Eragrostoideae respectively above and below 30 per cent. are superimposed on a map of the world showing those regions with the following combination of characters:

(i) Extremely arid, arid, or semiarid.
(ii) Precipitation in summer or without distinct season.
(iii) Mean temperature of coldest month above 10°C.

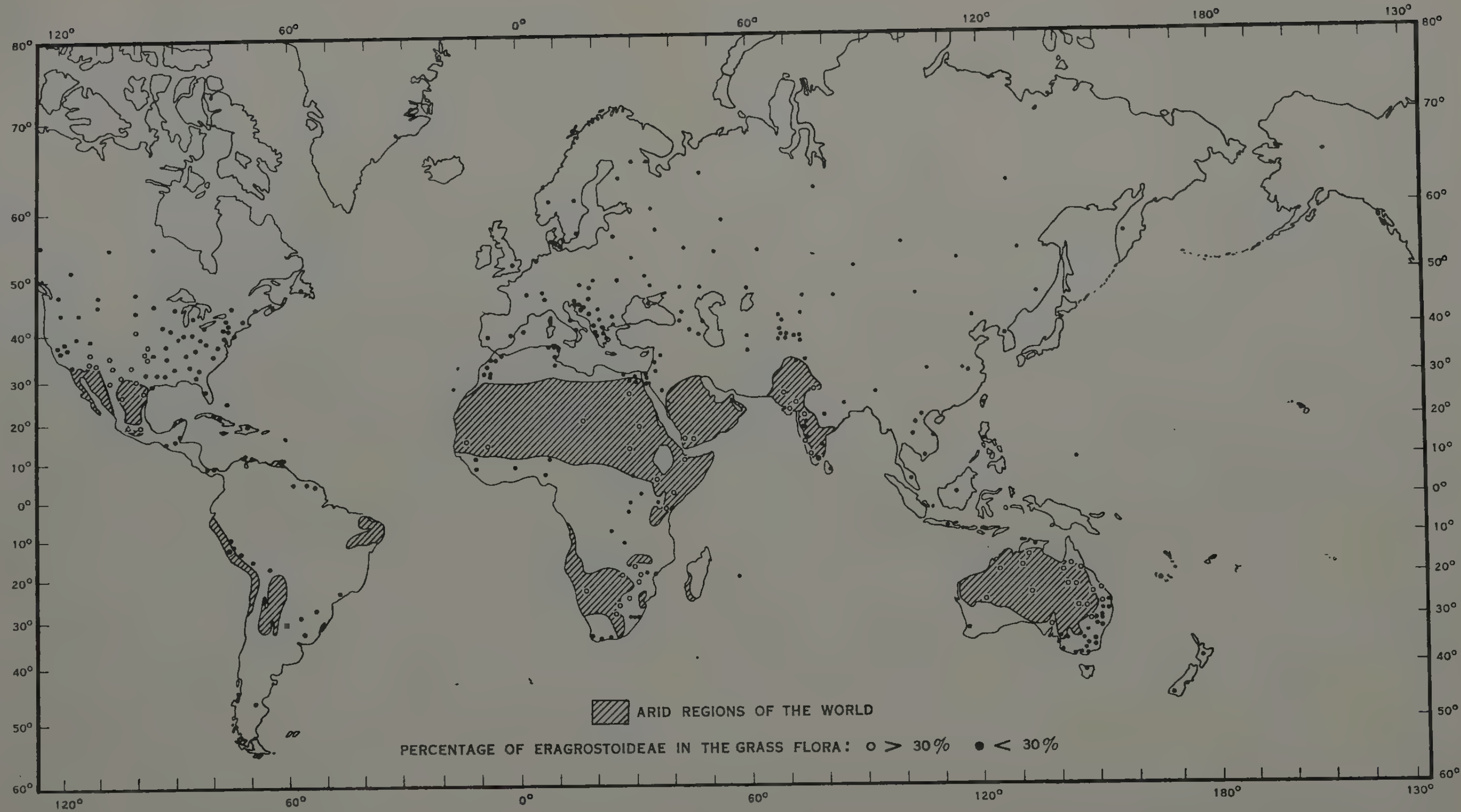
ARID REGIONS OF THE WORLD
PERCENTAGE OF ERAGROSTOIDEAE IN THE GRASS FLORA: ○ > 30% ● < 30%
120°
60°
0°
60°
120°
180°
130°
80°
70°
60°
50°
40°
30°
20°
10°
0°
10°
20°
30°
40°
50°
60°

Fig. 4.—Map of the world showing the correlation between localities with more than 30 per cent. of species of Eragrostoideae in the total grass flora, and regions (shown hatched) having the following combination of climatic characters (Meigs 1953): (i) Extremely arid, arid, or semiarid (types E, A, and S); (ii) Non-seasonal or summer precipitation (types a and b); (iii) Mean midwinter temperature above 10°C (types 2 and 3).

In most parts of the world there is a striking correspondence between the occurrence of high percentages of Eragrostoideae and the combination of climatic characters indicated above. This is particularly evident in Africa, and to an almost equal degree in Australia. In India, all localities with percentages of species of Eragrostoideae exceeding 30 occur within, or marginal to, the climatic zone indicated, but some lower values also occur within this zone. Conversely, in North America the percentage of Eragrostoideae always exceeds 30 within the climatic zone indicated, but high values are also found in some localities north of it. The data in South America are too scattered and fragmentary for any firm conclusions to be drawn.

TABLE 4

REGIONS WITH HIGHEST PERCENTAGES OF SPECIES OF ERAGROSTOIDEAE

Region	No. of Grass Spp.		Per Cent. of Eragrost.	Reference
	Total	Eragrost.		
South West Africa	203	121	59·6	Pilger 1954*b*
Tibesti, Sahara	95	52	54·7	Quezel 1958
Jornada Exp. Range, New Mexico	84	43	51·2	Little and Campbell 1943
North-eastern Sonora, Mexico	137	69	50·4	White 1948
Queensland: Bourke district	234	97	47·9	Queensland Herbarium
Western British Somaliland	98	46	46·9	Hubbard 1941
Texas: Trans-Pecos area	197	92	46·7	Cory and Parks 1937
Queensland: Maranoa district	150	69	46·0	Queensland Herbarium
Central Australia	138	62	45·0	Chippendale 1959
Bombay: Sind region	83	37	44·6	Blatter and McCann 1935
Orange Free State	139	62	44·6	Mostert 1958

The influence of winter temperature and seasonal distribution of rainfall is particularly apparent in North Africa. Almost all this region has an arid or semi-arid climate, but with the change to predominantly winter precipitation north of about latitude 30° N., the percentage of species of Eragrostoideae falls off rapidly. Similarly, there is an extensive arid region east of the Caspian Sea, but the low winter temperatures and predominantly winter rainfall preclude the development of high concentrations of Eragrostoideae. However, the occurrence in this region of a zone in which the percentage frequency of species of the subfamily exceeds 10 (cf. Fig. 3) may reflect the effect of aridity.

The extension of the zone of high concentration of Eragrostoideae northwards into the central southern United States (Kansas, Oklahoma, and New Mexico) is of interest as showing a deviation from the climatic relationships which occur elsewhere. Most of this region has an arid or semiarid climate, with rainfall predominantly in summer, but the mean temperature of the coldest month is usually below 10°C. The relatively high percentage frequency of the subfamily in this region is largely attributable to the occurrence there of many species of *Muhlenbergia*. As shown in Table 3, the subtribe Muhlenbergiinae has its highest concentration in a zone from central Mexico to Nebraska. As a whole, it appears to be more tolerant of low winter temperatures than other taxa of the Eragrostoideae.

While the evidence presented above indicates a close relationship between the distribution of the Eragrostoideae and climatic factors, it cannot be concluded that the particular climatic factors discussed are the only ones concerned, or that they operate independently. The effect of winter temperature appears to be well marked, and, with the exception of the central United States, consistent throughout the world. However, the degree of aridity and the seasonal distribution of the rainfall tend to be associated in the warmer parts of the world. Areas of very arid climate have predominantly summer or non-seasonal rainfall. Within these regions, also, the rainfall is markedly erratic, in contrast to the more reliable rainfall of the Mediterranean climates. Many of the grasses of the subfamily Eragrostoideae are especially adapted for growth under conditious of erratic rainfall. Annuals—frequently semi-ephemerals—are common, as are perennials with special adaptations enabling them to withstand prolonged drought. Since, however, they lack the ability to make active growth during the cooler months of the year, they do not succeed in the regions of Mediterranean climate where summer drought is counterbalanced by moist winters.

VI. The Distribution of Controversial Genera

As noted above, the subfamily Eragrostoideae used in this study is based on Pilger's classification, modified by the inclusion of the Pappophoreae and the exclusion of the Garnotiinae and the Phaenospermeae. It has been shown that the distribution of the Pappophoreae fits well into the pattern of climatic response characteristic of the subfamily, while conversely the genera *Garnotia* and *Phaenosperma* occur in regions of very different climate. There remain several other controversial genera, the relationships of which have been in dispute among taxonomists. Some of these are included in the Eragrostoideae by Pilger, while others have been excluded. It is interesting to consider the distribution of the more important of these genera compared with the geographical and climatic distribution pattern of the subfamily.

(*a*) *Triodia* and *Plectrachne*

These two genera, which are closely related, were excluded from the Eragrostoideae by Pilger, but have been placed in the Eragrosteae by many other authorities. Their relationships have been discussed by Burbidge (1953), who concludes that they are most logically placed with *Sieglingia* in the tribe Danthonieae as defined by Hubbard. The latter is a small tribe, the distribution of which has not been studied in detail. However, the inclusion of these two genera in the Eragrostinae would not greatly change the pattern of geographical distribution. Both are indigenous to Australia and occur in the more arid regions (Burbidge 1953). Their inclusion in Figure 1 would have the effect of raising the percentage of species of the subtribe in inland Australia. In particular, the percentage for the Alice Springs region would be raised to 26·8. Thus the geographical evidence is consistent with the inclusion of these two genera in the Eragrostinae.

(*b*) *Astrebla*

The genus *Astrebla* shows some affinities with *Triodia*, discussed above, and also with *Danthonia* (Hubbard 1928). It has usually been placed in the Chlorideae, but was included with *Triodia* in the Festuceae subtribe Triodiinae by Pilger. Tateoka (1957*b*) has shown that in chromosome size and number, as well as in leaf structure, *Astrebla* is allied to the Chlorideae rather than to the Festuceae.

This conclusion is supported by the geographical evidence. The genus is exclusively Australian, with its best development in the hot, arid regions of summer rainfall, which, as shown above, are those in which the Eragrostoideae are most characteristically developed.

(*c*) *Spartina*

This genus has usually been placed in the Chlorideae by taxonomists, but was raised to the status of an independent tribe, Spartineae, by Clapham, Tutin, and Warburg (1952). It was excluded from the Eragrostoideae by Pilger, and placed by him in the Phalarideae. *Spartina* has recently been the subject of a monograph by Mobberley (1956), who leaves it in the Chlorideae while commenting: "In no other particulars of the inflorescence, except in the character linking all members of the subfamily Festucoideae, does *Spartina* agree with the other genera referred to the Chlorideae".

The genus occurs principally along, and adjacent to, the Atlantic coasts of North and South America, Europe, and Africa. Typically the species occupy rather specialized habitats of coastal and inland salt and fresh marshes, and sand dunes. In geographical distribution and climatic response, the genus differs greatly from the general pattern of the Eragrostoideae, and the recent tendency to remove *Spartina* from that subfamily is supported by the geographical evidence.

(*d*) *Cleistogenes* and *Neyraudia*

The first of these genera was placed by Pilger in the Arundineae and the latter in the Eragrosteae–Eragrostinae. Other authors have placed both genera in the Arundineae or, alternatively, both in the Eragrosteae. Tateoka (1956*a*, 1956*b*) took the opposite view to Pilger, placing *Cleistogenes* in the Eragrosteae and *Neyraudia* in the Arundineae, largely on the basis of leaf structure. In a recent monograph of the two genera, Conert (1959*b*) supports the earlier view of Hubbard (1936) that both should be placed in the Eragrosteae.

In geographical distribution the two genera do not fit well into the pattern of the Eragrostoideae. *Cleistogenes* has 10 species in southern and south-eastern Europe and in northern and central Asia. Most of these species occur in regions of cold winters, such as Manchuria and adjacent parts of northern China and Mongolia. Few, if any, other genera or species of the subfamily occur in regions of comparable climate.

On the other hand, the four species of the small genus *Neyraudia* occur in tropical regions of relatively high rainfall, from southern China and Indonesia to Madagascar and Tanganyika. This distribution is not altogether inconsistent with that of other taxa of Eragrostoideae, but the inclusion of *Neyraudia* in the subfamily is not supported by the geographical evidence.

(*e*) *Beckmannia*

This very small genus has usually been included in the Chlorideae because of the arrangement of the spikelets on one side of the panicle branches. However, histological and cytological studies have shown that the genus has little relationship to this tribe. The affinities of *Beckmannia* have been discussed by Reeder (1953), who concluded that it should be placed in the tribe Agrostideae. Pilger also removes the genus from the Chlorideae, but places it as a separate subtribe of the Festuceae.

It may be noted that the geographical evidence supports the removal of *Beckmannia* from the Chlorideae. Of the two species, one is native to Europe, and the other to North America and temperate Asia. Neither are plants of arid regions.

VII. THE ORIGIN AND EVOLUTION OF THE ERAGROSTOIDEAE

The close relationship shown to exist between climatic factors and the distribution of the subfamily Eragrostoideae throughout the world suggests that the subfamily is an old one, the present distribution of which (on the broad basis considered here) is not greatly affected by historical factors. While particular tribes and subtribes, and especially individual genera, have a more restricted distribution, the subfamily as a whole appears to have spread widely throughout the parts of the world to which it is climatically and physiologically adapted, and to have achieved a state of balance with the environment. As noted in discussing the subtribe Eragrostinae, many of the larger genera have a very wide distribution, extending over more than one continental area. Further, it is characteristic of the subfamily that many of the smaller genera, as well as many individual species, have a markedly disjunct distribution. Both these facts support the conclusion that the taxa concerned are old ones with a long evolutionary history.

Because of the wide distribution of many of the taxa, and the fact that there is no single major centre of relative specific differentiation, only tentative conclusions can be drawn from this study about the probable centre of origin of the subfamily. More than half (58) of the 104 genera included in the subfamily by Pilger (1956) after excluding the Garnotiinae and Phaenospermeae, occur in Africa, the corresponding numbers for the other continents being Asia 40, America 46, and Australia 23. Perhaps a better picture of generic distribution may be obtained from Table 5, based also on the data of Pilger (1956). As might be expected because of its geographical isolation, America has the largest number of endemic genera. However, many genera are confined to Africa, and, of the genera occurring in more than one continent, all—with a single exception—are found in Africa.

It appears possible, therefore, that the Eragrostoideae may have originated on the African continent, and spread from this region to other parts of the world. This tentative conclusion is supported by several other considerations:

(i) The Eragrostoideae are taxonomically related to the Panicoideae, which are believed to have originated in the East Africa–Madagascar area (Hartley 1958*b*).

(ii) As with the Panicoideae, there appears to be a major centre of endemism of Eragrostoideae in Madagascar, four genera (*Viguirella*, *Sclerodactylon*, *Neostapfiella*, and *Decaryella*) and many species being confined to this region.

(iii) With the exception of the Muhlenbergiinae, all the larger tribes and subtribes of the Eragrostoideae have centres of high specific differentiation on the African continent (Fig. 2).

TABLE 5

DISTRIBUTION OF GENERA OF THE ERAGROSTOIDEAE

Data from Pilger (1956)

Distribution	No. of Genera
Africa only	23
Asia only	8
America only	30
Australia only	7
Africa and Asia	13
Africa and America	3
Africa and Australia	1
Asia and America	1
Africa, Asia, and Australia	6
Africa, Asia, and America	3
Cosmopolitan	9

(iv) The subtribe Eragrostinae shows many characters regarded as primitive in the grass family, and is believed to be the group from which the other tribes and subtribes of the subfamily may have evolved. It was probably differentiated not later than the Oligocene (Rozhevits 1945). Evidence for an African origin of this subtribe includes:

(*a*) The subtribe is strongly represented on the African continent, 28 of the 40 genera occurring there.

(*b*) Monographers of some of the genera of the subtribe have concluded that these have probably originated in Africa. Lorch (personal communication), who has made an intensive study of *Dactyloctenium* and allied genera, concludes that these, and probably the whole subtribe Eragrostinae, may have originated in east tropical Africa.

(*c*) Some of the species showing primitive characters and apparent affinities to other tribes of grasses occur in Africa. Thus Mimeur (1951) has shown that *Eragrostis tholloni* and species of the section *Platystachia* of *Eragrostis*, all native to tropical and South Africa, closely resemble the genus *Briza* of the tribe Festuceae.

If, as surmised, the Eragrostoideae originated in east tropical Africa, this must have been at a very early stage in the evolution of the grass family. Such an early origin would be consistent with the present wide, and climatically balanced, distribution of the subfamily. The differentiation of the Eragrostoideae may have preceded the separation of the Panicoideae and Andropogoneae from the general panicoid stock, for, as shown in previous papers (Hartley 1958*a*, 1958*b*), these two tribes have not attained a distribution which is climatically balanced in the different hemispheres.

Some of the larger tribes of the Eragrostoideae are as widely distributed as the subfamily itself, and probably became differentiated at a very early period. Others, such as the subtribe Muhlenbergiinae and some of the smaller tribes, have a more restricted distribution, and may have originated later when it had already spread away from its centre of origin. Perhaps, too, this later evolution may have been associated with some change in the pattern of climatic response, as has been suggested in discussing the distribution of the genus *Muhlenbergia* in America. Whether this changing response represented a major evolutionary trend or a *cul-de-sac* can only be discussed when the distribution of the other tribes and subfamilies of the Gramineae has been investigated.

The intimate relationship between taxonomy and geographical distribution in the grass family is evident from the present study. As noted above, most of the genera which now form the subtribe Eragrostinae were included with the Festuceae by earlier botanists, while the other genera of the subfamily were variously distributed among widely separated tribes. With such a classification, no clear-cut relationship between distribution and climate could have been shown to exist. It was only with the recognition of the Eragrostinae (as the tribe Eragrosteae) by Hubbard as a taxonomically distinct entity that the relationship between distribution and climate began to emerge. This relationship is still imperfect, as has been shown in Section III of this paper. The work of later taxonomists, in helping to clarify the relationship between the Eragrostinae and other subtribes and tribes now comprised within the subfamily Eragrostoideae, has at the same time made possible the demonstration of a more precise and clear-cut relationship between distribution and climate. This in turn has reciprocal value for the taxonomist, for, as has been indicated in discussing the Phaenospermeae, Garnotiinae, and some of the controversial genera, deviations from the expected distribution–climatic pattern may throw doubt on the reality of suggested taxonomic affinities.

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DESTRUCTION OF INDIGENOUS HEATH VEGETATION IN VICTORIAN SEA-BIRD COLONIES

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Summary

The sclerophyllous heath and scrub which occupies undisturbed granite coasts is essentially a vegetation of infertile, acid soils deficient in available phosphorus and nitrogen and sometimes in potassium and certain microelements. In sea-bird colonies soil reaction and fertility are altered by the deposition of guano, which is rich in phosphorus, nitrogen, and potassium, and the indigenous heath and scrub are destroyed. Mechanical disturbance and chemical changes hinder the accumulation of surface peat.

Toxicity of guano in summer leads to a specialized flora and limits the total number of species. Comparison of floristic data from sea-bird islands and nearby control areas with no nesting sea-birds illustrates the widely divergent nature of the flora in the two habitats.

Heath species are almost non-existent in the rookeries, and sclerophylls, switch plants, and woody plants much rarer than in the control areas. Conversely, succulents, annuals, biennials, and aliens are considerably more abundant in the rookeries. Man is the primary introducer of alien plants; but gulls are also important in this respect, and all colonial sea-birds make the habitat more suitable for invasion

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by ruderals in the autumn when mechanical disturbance ceases and guano becomes diluted to beneficial concentrations.

Where man has access to the rookeries large areas may become dominated by introduced weeds which are seldom able to establish themselves on unmodified heath soils.

The vegetation of sand dunes (to which few nutrients are being added and from which few have been leached) lies between that of the leached soils of heaths and the guano-rich soils of rookeries overlying granite in all the above characters, in spite of the markedly different physical nature of the substratum, and contains a higher proportion of creeping plants than either.

Guano and sea salt have parallel effects on vegetation, and the presence of sea-birds leads to a broadening of the coastal belt of salt-resistant plants and elimination of the indigenous, more inland type of flora. *Pteridium esculentum* and *Leptospermum laevigatum* are important species in the transition zone between either saline or guano-rich habitats and the surrounding heath.

I. Edaphic Characters of Typical Heathland

Specht and Rayson (1957) state that the sclerophyllous understorey vegetation of southern and eastern Australia occurs consistently on soils of very low fertility. These they describe as being always acid and very low in available phosphorus and nitrogen and sometimes in potassium and the microelements copper, zinc, and molybdenum.

This sclerophyllous understorey is the vegetation which dominates the unspoiled coastal granite communities of Victoria and Tasmania—either as low sea-bird heath or as wind-resistant scrub. Very few sclerophylls, however, persist in sea-bird rookeries studied on nine granite islands of south-eastern Victoria (Gillham 1960*a*, 1960*b*).

Rookery soil is neither infertile nor acid, nor does it lack the macronutrients phosphorus, nitrogen, and potassium, all of which are important constituents of guano. It is not surprising, therefore, that the sclerophyllous plants give way to other, more demanding species in the rookeries.

Wood (1939) stresses the edaphic factor in the classification of plant communities, and shows the importance of phosphorus, nitrogen, and soil pH in governing the limits of eight plant communities in South Australia. As rookery vegetation and that of adjacent heathlands frequently suffer the same degree of wind exposure and other physical factors of the environment, there seems little doubt that the replacement of the indigenous heath in the rookeries is due to edaphic modifications brought about by the birds.

II. Effect of Guano on Soil Reaction and Soil Nutrients

The importance of guano rather than burrowing and other soil disturbance by the birds in the elimination of heath vegetation in these latitudes is illustrated by the smaller degree of damage perpetrated in the higher-rainfall areas where the rate of leaching is greater. In Victorian habitats heath species are extremely rare in bird colonies. As southern and western Tasmania are approached, progressively more heath species are able to survive in rookeries until, on the west coast, sparsely inhabited colonies of mutton birds are found in almost unmodified heath communities. Not only is guano rapidly washed from the soil under these conditions and less often maintained at a toxic concentration by high evaporation rates, but the climate is more conducive to peat accumulation, so that much of the guano will be held by the retentive surface layers and have little effect on the soil solution around the absorptive roots below (Gillham 1956, 1960*c*).

It is hoped to deal with this question in greater detail in relation to the Tasmanian rookeries in a subsequent publication. The present work on the Victorian islands serves to illustrate the striking differences between flora affected by birds and flora not so affected, in a climatic region where differences are more marked than in many parts of Tasmania.

Guano has two major roles, one in the modification of soil pH, and the other in the addition of nutrients. In general the soil reaction becomes more alkaline in the presence of guano, although this may be masked in the more exposed habitats by chemical interaction with constituents of sea spray (Gillham 1956).

Average moist guano may contain 9–18 per cent. of nitrogen, 9–14 per cent. of phosphoric acid, 2–6 per cent. of potash, and 6–11 per cent. of lime, these being the four macronutrients most commonly added to heath soils by agronomists in order to get growth of grasses and clovers. The agronomist, however, first destroys the heath vegetation by fire or some mechanical means. In the rookeries it would seem that centuries of guano deposition, coupled with the mechanical effects of digging and trampling by the birds, have brought about a more effective destruction, where persistent sclerophylls no longer regenerate from surviving underground organs as in sown pasture.

III. Disturbance of Surface Peat by Burrowing Birds

Excavating birds tend to destroy the surface litter layer, scattering some, dragging some of the undecayed components underground to the nesting chamber, and burying much of the remainder beneath mineral soil thrown out from below. In addition both high pH and nitrogen content hasten decomposition (Crocker 1959), so that peat does not accumulate so readily in the rookeries.

A surface layer of peat is not so characteristically associated with dry heath vegetation in Victoria as in cooler, moister areas, however, and the sclerophylls of the control areas studied in this investigation grow on sand fairly free from organic matter. The displacement of soil organic matter in both rookeries and control areas is likely to be facilitated by the dispersing effect of blown sea spray.

IV. Effect of Occupation by Birds on the Total Species Number

The specialized environment of the bird colonies in summer lies outside the range of tolerance of the majority of plants, mesophylls and sclerophylls alike, and leads to a limited and specialized flora.

It was very apparent during the unusually dry summer of 1959 that the rigours of the habitat were aggravated by drought and were much alleviated in the higher-rainfall areas of southern and western Tasmania, particularly on southward-facing slopes.

The intensification by drought of the adverse environment created by the birds in summer would appear to be largely due to two factors:

(i) High evaporation rates, leading to toxic concentrations of guano in the soil instead of progressive dilution and leaching.

(ii) Wilting of the lush growths of soft-leaved plants, which replace the xeromorphic sclerophylls of the indigenous heath owing to the more favourable soil conditions of the less adverse winter season, but which are less well fitted to combat drought. It is the inability of many coprophiles to survive through the summer which leads to the strong ephemeral element in rookery vegetation.

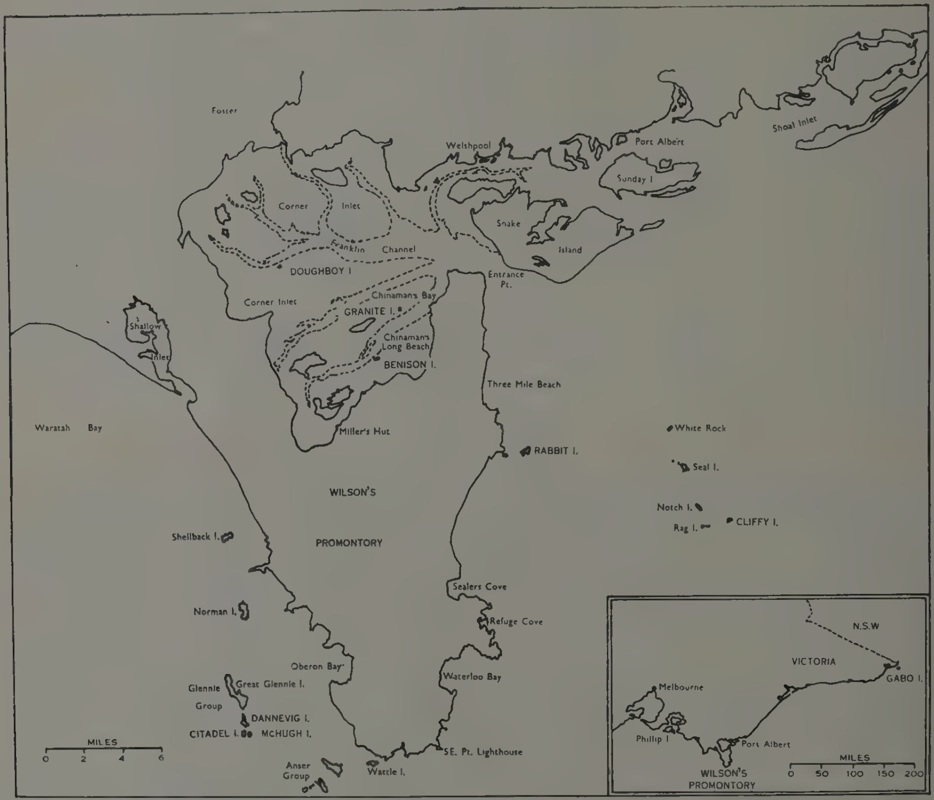
Foster
Welshpool
Port Albert
Shoal Inlet
Sunday I
Corner
Inlet
Snake
Island
Franklin
Channel
DOUGHBOY I
Entrance Pt.
Corner Inlet
Chinaman's Bay
GRANITE I.
Shallow
Inlet
Chinaman's Long Beach
BENISON I.
Three Mile Beach
Waratah Bay
Miller's Hut
White Rock
RABBIT I.
Seal I.
WILSON'S
Notch I.
Rag I.
CLIFFY I.
Shellback I.
PROMONTORY
Sealers Cove
Norman I.
Refuge Cove
Oberon Bay
Waterloo Bay
Glennie Group
Great Glennie I.
DANNEVIG I.
CITADEL I.
MCHUGH I.
SE. Pt. Lighthouse
MILES
0 2 4 6
Anser Group
Wattle I.
N.S.W
VICTORIA
GABO I.
Melbourne
Phillip I
Port Albert
WILSON'S PROMONTORY
MILES
0 50 100 150 200

Fig. 1.—Map of Wilson's Promontory and (*inset*) south-eastern Victoria, showing position of bird islands.

An analogy may be drawn with the soft-leaved ephemerals which spring up on the saline soils of the inland after rain, particularly on the sandier soils, and die away to leave a "skeleton flora" of hardy perennials.

Analogy may also be drawn between the "skeleton floras" of the two habitats. The chief perennating life form in the bird colonies of south-eastern Australia is that of *Poa poiformis* and *Stipa teretifolia*, wiry-leaved grasses of the desert "spinifex" (*Triodia*) type. Second in importance are succulent-leaved, woody-stemmed members of the Aizoaceae and, less important, the Chenopodiaceae, a life form represented by the saltbushes of the interior. Thirdly, there are the sclerophyllous shrubs, exemplified on the one hand by the coastal tea-trees and on the other by mulga etc.

These three life forms occupy almost the entire area on the three small islands of the Glennie group—the most adverse of the plant habitats investigated, as far as exposure to wind and spray and erodibility of shallow soil are concerned. The deposition of salt spray here adds to the concentration of soil salts brought about by guano and the shallow nature of the soil aggravates the effects of drought. Only 26 species were found on the three islands, compared with 105 on an area of approximately equal size and exposure on the adjacent mainland coast, or 74 excluding areas of dune sand.

In areas where plant growth was less severely inhibited by climatic and edaphic factors, the purest stands of "skeleton species" were found in grazed habitats, i.e. in the almost pure *Poa poiformis* tussock of Rabbit I. and the equally pure *Carpobrotus rossii* swards of Gabo I. (see Fig. 1).

Like wind, salt spray, and soil drought, grazing animals contribute to the same type of "resistant" flora. The soft-leaved mesophytes are again the first to succumb to their attentions, the rigid-leaved grasses and unpalatably salty *Carpobrotus* remaining relatively unscathed. (Observations suggest that *Carpobrotus* is seldom grazed, and *Disphyma* and *Tetragonia* are eaten more readily when growing in the less saline soils.)

The number of species recorded on the 80–100 acres of Rabbit I. was only 24, whereas 70 were found on the Three Mile Beach control area nearby. Relevant figures for Gabo I. are 60 rookery species and 118 control area species, whilst Benison and Granite Is. show 64 species as against 137 on the adjacent mainland coast.

These figures are not directly comparable, because the areas examined are not of exactly the same size and because lists made during a drought summer must, of necessity, be very incomplete, but they diverge widely enough to show the significance of the summer repression of the flora in the rookeries.

Species frequency figures for the two habitat types are listed in Table 1. The curves, expressed as percentages, follow each other fairly closely, but that for the bird islands lies below the other for the 100–40 per cent. frequency categories and above it for the 30–10 per cent. categories.

The smaller proportion of species showing a high percentage frequency illustrates the simplicity of the rookery flora, with its overwhelming dominance of one or a few species instead of the mixed dominance which is often seen on coastal heaths. The larger proportion of adventive or casual species in the lower frequency categories illustrates the suitability of the rookeries for "weed" establishment.

On Doughboy I. floristic analyses of equal areas of burrowed and unburrowed soil reveal more than three times as many species in the latter (7 and 23 species respectively on 14 sq. m) (Gillham 1960*b*, Fig. 1). Most of this rookery is covered by almost pure stands of *Carduus tenuiflorus*, *Senecio* spp., or *Vinca major*, or a combination of these.

Diffuse guano deposition in sparsely populated rookeries may be beneficial; otherwise the presence of sea-birds must be regarded as generally inimical to plant life in summer, unless rainfall is sufficient to offset its effects. Where sea-birds are associated with three other suppressive factors often encountered on the bird islands, viz. exposure to wind and spray, shallow soil, and rabbit grazing, the paucity of species is remarkable—as on Citadel I., where only seven species of flowering plants and two ferns were recorded on 70 acres, giving a species : acreage ratio of 1 : 8 (Gillham 1960*a*).

Table 1

SPECIES FREQUENCY INSIDE AND OUTSIDE THE ROOKERIES

Total number of species recorded, 360

Percentage Frequency Category	Number of Species		Percentage of Species	
	Bird Islands	Other Areas	Bird Islands	Other Areas
100	—	1	—	0·3
90	2	5	1·2	1·6
80	1	5	0·6	1·6
70	4	12	2·4	3·9
60	3	10	1·8	3·2
50	6	16	3·6	5·1
40	10	25	6·0	8·0
30	19	35	11·4	11·2
20	37	55	22·2	17·6
10	84	148	50·8	47·5
Total	166	312	100	100

V. CONTROL AREAS FOR CONTRAST OF COASTAL VEGETATION INSIDE AND OUTSIDE THE ROOKERIES

Control areas unaffected by nesting sea-birds were selected as close as possible to the rookeries under investigation, and the flora of the two sets of habitats compared. Results are set out in Appendix I and in Figures 2 and 3, where it will be seen that the vegetation types in the control areas are closely similar to each other but differ widely from those of the nearby rookeries.

Exposure to spray-bearing winds, parent soil type, and other environmental factors vary little between members of each pair of habitats, and it is reasonable to attribute the divergence to the presence or absence of sea-birds. In six instances the areas investigated as the control zones are approximately equal in size to the islands with which they are compared, and do not extend far from the coast where conditions of exposure might be materially different. In the seventh geographical zone, Mallacoota, near Gabo I., the "rookery area" consists merely of a few metres of ground beneath a dead *Melaleuca ericifolia* branch used as a bird perch. The sudden transition from the woody sclerophylls of the surrounding heath to the lush succulents which characterize the Gabo I. penguin rookery is sufficiently striking to merit the separate treatment of this tiny oasis of bird flora so far from the coast. Eight of the 10 species occurring were not recorded elsewhere in this heath community, except on the disturbed soil around a rubbish tip where a similar but less marked destruction of the native heath flora had occurred locally. Only three were found on the coastal dunes.

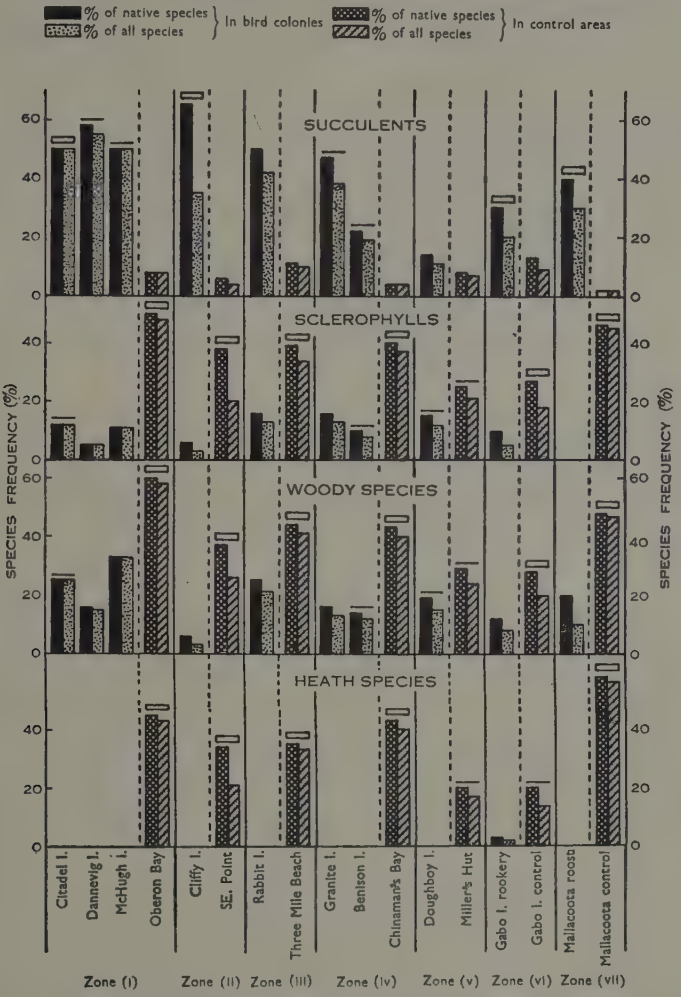

Fig. 2.—Distribution of succulents, sclerophylls, woody species, and heath species in bird colonies and control areas, south-eastern Victoria. Double horizontal line above species frequency column indicates dominance of a life form; single line indicates local dominance.

Such a clearly defined change brought about by only one or a few birds (species unknown) is illustrative of the significance of guano in the determination of vegetation type, even where unaccompanied by burrowing and trampling.

The seven geographical zones in which comparisons are made are indicated in Figure 2 and Table 2 (see also map in Fig. 1).

In all control areas the vegetation is sclerophyllous scrub or low mixed heath, dominated in the granite areas by *Banksia marginata*, *B. integrifolia*, *Casuarina distyla*, *C. stricta*, *Leptospermum laevigatum*, *L. juniperinum*, and *Myoporum insulare*, with *Banksia serrata* and *Melaleuca ericifolia* on the sheltered Corner Inlet coast, and *Acacia longifolia*, *A. sophorae*, and *Helichrysum gunnii* in the sandier areas. Rookery floras, both granitic and sandy, are almost entirely herbaceous, apart from some *Melaleuca ericifolia* on the two most sheltered islands. The principal species are *Carduus tenuiflorus*, *Carpobrotus rossii*, *Disphyma australe*, *Pelargonium australe*, *Poa poiformis*, *Senecio lautus*, and *Vinca major*.*

VI. Distribution of Heath Species

Plants which are typically present on coastal heath, but not necessarily confined to this type of habitat, are indicated in Appendix I, and their distribution shown in the lowest series of histograms in Figure 2.

No true heath species were found on the eight islands around Wilson's Promontory, in spite of the overwhelming dominance of this group of plants on both sheltered and exposed parts of the adjacent mainland coast. None were recorded beneath the Mallacoota bird roost in typical *Leptospermum juniperinum–Melaleuca ericifolia* scrub, and only one (*Amperea spartioides*) in the Gabo I. rookery, this being scarce and marginal.

The data graphed refer only to the number of heath species present, not to their relative abundance. Depiction of the percentage ground cover would have shown much greater differences between mainland and islands, as the heath species, although not amounting to more than 53 per cent. of the total number in any of the mainland habitats, occupied most of the ground. Of the 312 species recorded in the control areas 23·2 per cent. may be regarded as true heath species, but only 0·2 per cent. of the 166 rookery species. This same wide divergence between rookery and heath vegetation is seen on the Western Australian aeolianite (Gillham 1960*d*).

VII. Distribution of Plant Life Forms Inside and Outside the Rookeries

(*a*) *Sclerophylls*

Nitrogen deficiency leads to the production of small cells and an apparent xeromorphy in plants, so a higher proportion of sclerophyllous species is to be expected on the nitrogen-deficient heath soils than on the guano-impregnated soils of the rookeries.

The columns in Figure 2 for sclerophylls and switch plants resemble those for heath species, but the differences are less sharply defined, because a number of coastal shrubs, bracken, etc. fall within the category of sclerophylls (i.e. "plants having hard and stiff leaves"). These, although not infrequently present in the rookeries, seldom constitute the dominant species there.

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* Ecological accounts of rookeries and control areas have been lodged at the Melbourne University Botany School and the Wildlife Survey Laboratory, C.S.I.R.O., Perth.

Xeromorphy is a genetically fixed character in many heath plants, but there is a tendency for some to show larger leaves than normal when growing in the more fertile soils.

The average percentage of sclerophylls in the rookery flora is 8·2 per cent.; in the control areas 32·0 per cent. (ratio 1 : 3·9).

(*b*) *Woody Plants*

Much the same type of distribution is seen among woody species, although these, particularly in the rookeries, are not necessarily sclerophylls and include soft-leaved species such as *Solanum aviculare* and *Muehlenbeckia adpressa* and succulent-leaved species such as *Rhagodia baccata.* The anomalously low proportion of both this group and the last on the three lighthouse stations (Cliffy I., Gabo I., and in the south-east of Wilson's Promontory) is more probably due to the high proportion of herbaceous aliens than to fuel cutting.

The average percentage of woody plants in the rookeries is 15·5 per cent.; in the control areas 36·6 per cent. (ratio, 1 : 2·4).

(*c*) *Succulent Plants*

The opposite trend is seen among succulent plants, which not only cover a great deal more ground in the bird colonies, but include a greater variety of species there than in the control areas. The average percentage of succulent species in the rookeries is 35 per cent.; in the control areas 6·6 per cent. (ratio, 5·3 : 1).

(*d*) *Xeromorphic Monocotyledons*

Xeromorphic monocotyledons, principally *Poa poiformis*, cover a great deal more ground in the rookeries than in the control areas—replacing the sclerophyllous undershrub as the dominant life form. The group is represented in the heath flora, however, by a number of less conspicuous species, so that the difference in the number of species, as compared with ground cover, is small (8·7 per cent. and 9·9 per cent. in rookeries and control areas respectively) (ratio, 1 : 1·1).

(*e*) *Creeping Plants*

No significant difference is seen in the proportion of creeping plants in and out of the rookeries, the percentage frequencies being 25·6 and 29·0 per cent. respectively (ratio, 1 : 1·1).

(*f*) *Alien Plants*

Man is the principal agent in the introduction of alien plants to the islands, but birds also play their part. Gulls are omnivorous feeders and are undoubted agents in the dispersal of seeds (Gillham 1956); other sea-birds feed at sea, coming ashore only at the nesting site, so have no opportunity to introduce new species. They have, however, a function in the production of a suitable seed bed. By destroying existing plants and "tilling" and manuring the ground, they produce an "arable" habitat suitable for weeds of stockyards and waste places.

It is likely that the increased fertility is of most vital importance in the establishment of the newcomers (which are often confined to the disturbed soils of roadsides if present in heath country). Guano is rich in phosphorus, deficiency of which is a frequent cause of failure in alien plants introduced to heath soils by agronomists or foresters.

Only on those islands most remote from a source of disseminules (i.e. the Glennies) are aliens of little importance in the rookeries.

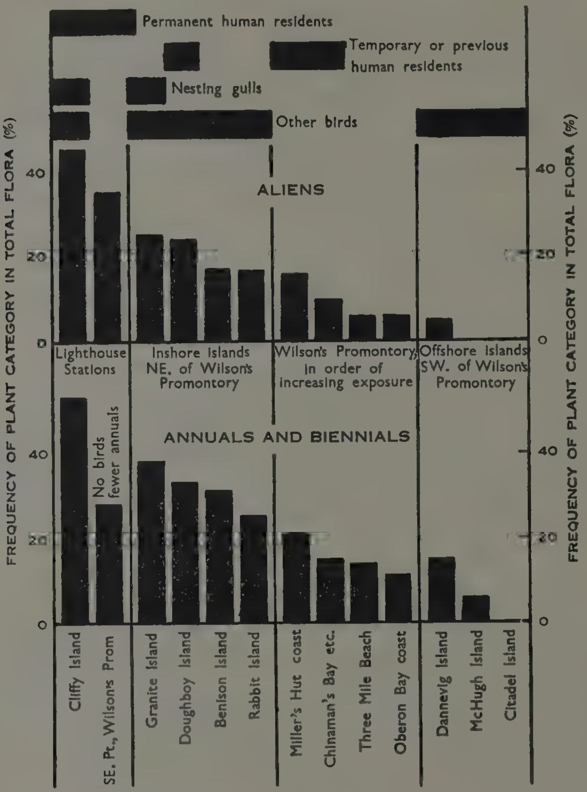

Fig. 3.—Percentage of introduced and short-lived plants in the Wilson's Promontory area in relation to disturbance by man, gulls, and other birds. Only the summer flora is shown, i.e. no account is taken of any influx of winter annuals in the rookeries.

The upper part of Figure 3 illustrates the distribution of alien species in the habitats on and around Wilson's Promontory in relation to the presence of man, of gulls, and of other nesting sea-birds.

The highest percentage of aliens (45 per cent.) was recorded on Cliffy I., where three lighthouse families reside and where gulls and other sea-birds nest. Wilson's Promontory Lighthouse Point, the only other permanent residence, but with no nesting sea-birds, ranked second with 35 per cent.; Granite I., the only other gull colony, ranked third with 25 per cent. On the mainland opposite Granite I. only 10 per cent. of aliens were recorded (6 per cent. in the granite control area, excluding dunes), in spite of the fact that the area is visited more often by man and includes a fairly well-frequented camp site.

Of the other two Corner Inlet islands Doughboy I., which had been previously inhabited and was still visited by picnic parties, showed a larger proportion of aliens than Benison I. (24 and 17 per cent. respectively) but slightly less than Granite I., which was too small for habitation but carried far more sea-birds per acre. (No nesting gulls were seen on Doughboy or Benison Is.)

Doughboy I. is the only one of the south-eastern Victorian series to which reference has been found in the botanical literature, and it seems that the number of aliens there has increased appreciably during the past 46 years.

A party from the Field Naturalists' Club of Victoria (A. J. Ewart, F. Pitcher, H. B. Williamson, and J. W. Audas), which visited the island in December 1912 and claim to have "scoured every corner of the island and made a complete collection of every flowering plant growing on it", recorded only six alien species (Kershaw *et al.* 1913). These represented 12 per cent. of their total of 50 plants.

In January 1959, 24 aliens were found, these representing 30 per cent. of the 80 species recorded and including the six which had been established previously. Ten of the newly recorded aliens were grasses and five were composites.

Kershaw *et al.* mention *Vinca major* and *Zantedeschia aethiopica* (then *Richardia africana*) as "having obtained a firm foothold". By 1959 a considerable number of others could be included in this category, particularly three locally dominant species not recorded at all in 1912 (*Carduus tenuiflorus*, *Aira caryophyllea*, and *Vulpia bromoides*). The *Vinca* was still firmly established, the *Zantedeschia* quite frequent but fairly scattered.

The lesson which is patently obvious, both here and on many of the more accessible bird islands in Tasmanian waters, is that where man has access to the fertile soil of the rookeries, the vegetation is likely to become radically changed, to the complete detriment of the native flora instead of merely to a different type of native flora. *Poa poiformis*, the commonest natural rookery dominant, was recorded on Doughboy I. only as isolated tussocks.

Considerable changes had occurred also in the native vegetation of Doughboy I. over the 46 year period, possibly as a result of the different type of competition encountered. Of the native species found in 1912, 22 were not seen in 1959, whilst 34 new ones were recorded, 20 of the more critical of these having been determined at the National Herbarium (see Appendix I).

Miller's Hut, the control area for Doughboy I., showed less than two-thirds of the percentage of aliens (14 and 24 per cent. of the combined 1912 and 1959 lists respectively), in spite of more recent habitation by man (14 and 30 per cent. of the 1959 records).

Three Mile Beach, the control area for Rabbit I., showed only one-third the proportion of introduced species (6 and 17 per cent. respectively) in spite of the proximity of an automatic light, and periodic visits by mechanics and trampers.

The Glennies are apparently too remote or too exposed, or both, for the arrival and establishment of aliens other than the widespread *Sonchus oleraceus*, which represents 4 per cent. of the total flora. The more complex flora of the Oberon control area also showed only 4 per cent., however, in spite of the fact that it included a track from the settlement by Tidal River to the north.

On Gabo I. the occupation of a lighthouse brought the figure for the control area closer to that for the bird colonies (rookery 33 per cent., control 29 per cent.), but at Mallacoota the figures diverged widely, although there was easy road access from the nearby holiday and fishing centre (bird roost 50 per cent., control 2 per cent., or 3 per cent. if the dunes are included).

The average percentage of aliens in the rookery flora of the seven zones is more than double that in the control areas (27 and 12·7 per cent. respectively (see Table 2).

Table 2

PRESENCE OF ALIENS AND ANNUALS (WITH BIENNIALS) IN ROOKERIES IN RELATION TO THOSE OF NEARBY CONTROL AREAS

Locality	Aliens (%)			Annuals and Biennials (%)		
	Rookery	Control	Ratio	Rookery	Control	Ratio
(i) Glennie Is. and Mount Oberon coast	4	4	1·0 : 1	17	7	2·4 : 1
(ii) Cliffy I. and SE. Wilson's Promontory (lighthouses)	45	35	1·3 : 1	53	27	1·9 : 1
(iii) Rabbit I. and Three Mile Beach	17	6	2·8 : 1	25	14	1·8 : 1
(iv) Benison and Granite Is. and Chinaman's Bay area	16	6	2·7 : 1	31	10	3·1 : 1
(v) Doughboy I. and Miller's Hut area	24	14	1·7 : 1	33	19	1·7 : 1
(vi) Gabo I. (lighthouse)	33	29	1·1 : 1	37	18	2·1 : 1
(vii) Mallacoota (Bastion Point)	50	2	16·7 : 1	30	4	7·5 : 1
Average	27·0	12·7	2·1 : 1	32·3	14·4	2·3 : 1

(*g*) *Annuals and Biennials*

The number of short-lived plants in the rookeries is also significantly larger than in the control areas, although only one in 10 of these was occupied by human habitation and its attendant ruderals, whereas two in seven of the control areas were so occupied.

As with aliens (which group embraced many of the annuals), the reason for this is likely to be twofold: the large area of available bare ground, and the more favourable soil reaction and nutrient status in the rookeries.

Had it been possible to visit the islands during the cooler, wetter months and record any winter annuals becoming established as the guano was diluted to a beneficial rather than a toxic concentration, the differences are likely to have been more striking. The average summer percentages for annuals and biennials were 26·8 per cent. in the bird colonies if recorded as 10 separate entities, 32·3 per cent. if recorded as seven geographical zones (see Section V). In the seven corresponding control areas 14·4 per cent. was recorded. (These figures take no account of the few perennials like *Senecio lautus*, which not infrequently behave as annuals in the cyclic rookery vegetation.)

Relevant figures for aliens and annuals in the seven zones are set out in Table 2.

Many of the annuals and biennials are also aliens (57 per cent. of the 79 species recorded). Of the 33 native annuals, 25 were found in the rookeries and only 18 in the control areas (see Appendix I).

TABLE 3

PRESENCE OF ALIENS AND ANNUALS IN HABITATS AFFECTED BY THE SEASONAL ACTIVITIES OF BIRDS AND THE NON-SEASONAL ACTIVITIES OF MAN, TO SHOW HIGHER PERCENTAGE OF ANNUALS IN THE FORMER

Records for all habitats * possessing more than 10 per cent. of aliens in the flora

Locality	Biotic Activity	Aliens (%)	Annuals and Biennials (%)	Ratio of Aliens to Annuals
Control Areas				
Gabo I. control area	Man	29	18	1 : 0·6
Wilson's Promontory, Lighthouse Point	Man	35	28	1 : 0·8
Miller's Hut coast	(Man)†	16	19	1 : 1·2
Bird Islands				
Gabo I. rookery	Birds and man	33	37	1 : 1·1
Cliffy I.	Birds and man	45	53	1 : 1·2
Doughboy I.	Birds (and man)†	24	33	1 : 1·4
Rabbit I.	Birds	17	25	1 : 1·5
Granite I.	Birds	25	38	1 : 1·5
Benison I.	Birds	17	31	1 : 1·8

* Excluding the small Mallacoota bush bird roost.

† No longer permanently inhabited.

The percentages of annuals and biennials in the habitats on and around Wilson's Promontory are graphed in the lower part of Figure 3 and show close agreement with the percentages of aliens.

The only real discrepancy is in the figures for the lighthouse point on Wilson's Promontory, and this would seem to be of some significance. In this area, introduction of alien plants has been due to the activities of man, and introduced perennials are not subjected to periods of intense disturbance and toxicity of soil solution as in the bird colonies in summer.

Where introductions are due to birds, either with or without the assistance of man, the annual element is more strongly represented, few of the mesophytic aliens being able to tolerate the rigours of combined bird activity and summer drought. Perennial introductions, other than of markedly coprophilous plants such as *Urtica* spp., tend to be suppressed in the rookeries in favour of the "bird evaders," whose dormant seeds are able to take advantage of the subdued fertility after the first autumn rains.

TABLE 4

ROOKERY SPECIES OF 40 PER CENT. FREQUENCY AND OVER (26 SPP.)

Percentage Frequency	Species	Aliens	Annuals/ Biennials	Succulents	Sclerophylls	Woody spp.	Heath spp.
90	*Poa poiformis*						
	Senecio lautus			(F)			
80	*Carpobrotus rossii*			F			
70	*Disphyma australe*			F			
	Crassula sieberiana		A	F			
	Lobelia anceps			F			
	Sonchus oleraceus	I	A	(F)			
60	*Bulbine semibarbata*			F			
	Pelargonium australe						
	Correa alba					W	
50	*Pteridium esculentum*				X		
	Vulpia bromoides	I	A				
	Atriplex hastata	I	A	(F)			
	Tetragonia implexicoma			F			
	Calandrinia calyptrata		A	F			
	Lavatera plebeja						
40	*Asplenium obtusatum*			F			
	Bromus diandrus	I	A				
	Scirpus nodosus						
	Muehlenbeckia adpressa					W	
	Rhagodia baccata			F		W	
	Salicornia australis			F			
	Sambucus sp.					W	
	Gnaphalium luteo-album		A				
	Cirsium vulgare	I	B				
	Hypochaeris radicata	I					
	Totals (%)	23	31	44	4	15	0
	Totals for 16 spp. of over 50% frequency (%)	19	31	53	6	6	0

This principle is equally well illustrated 320 miles to the north-east on Gabo I., where annuals, expressed as a percentage of aliens, amount to 112 per cent. in the rookery and only 60 per cent. in the control area.

TABLE 5

HEATH AND DUNE SPECIES OF 50 PER CENT. FREQUENCY AND OVER (48 SPP.)

Percentage Frequency	Species	Aliens	Annuals/ Biennials	Succulents	Sclerophylls	Woody spp.	Heath spp.
100	*Pteridium esculentum*				X		
90	*Scirpus nodosus*						
	Acaena anserinifolia						
	Acacia longifolia var. *sophorae*				X	W	
	Leptospermum laevigatum				X	W	
	Dichondra repens						
80	*Viola hederacea*						
	Epacris impressa				X	W	M
	Anagallis arvensis	I	A				
	Senecio lautus			(F)			
70	*Stipa teretifolia*						
	Lepidosperma concavum						M
	Banksia integrifolia				X	W	
	B. marginata				X	W	M
	Carpobrotus rossii			F			
	Oxalis corniculata						
	Correa alba					W	
	Hydrocotyle peduncularis						
	Apium prostratum			F			
	Monotoca elliptica				X	W	
	Centaurium pulchellum						
	Lobelia anceps			F			
60	*Agrostis avenacea*						
	Aira caryophyllea	I	A				
	Lepidosperma gladiatum						
	Xanthorrhoea australis					W	M
	Muehlenbeckia adpressa					W	
	Melaleuca ericifolia				X	W	
	Halorrhagis tetragyna?						M
	Leucopogon parviflorus				X	W	
	Helichrysum gunnii				X	W	
	Hypochoeris radicata						
50	*Poa poiformis*						
	Centrolepis strigosa		A				
	Lomandra longifolia						
	Casuarina distyla				S	W	M
	C. stricta				S	W	
	Tetragonia implexicoma			F			
	Crassula sieberiana		A	F			
	Acacia suaveolens				X	W	M
	Correa reflexa					W	M
	Amperea spartioides				X	W	M
	Leptospermum juniperinum				X	W	M
	Astroloma humifusum				X	W	M
	Myoporum insulare			(F)	(X)	W	
	Selliera radicans			F			
	Cirsium vulgare	I	B				
	Sonchus megalocarpus			(F)			
	Totals (%)	6	10	15	34	41	22

TABLE 6

OCCURRENCE OF SIX PLANT CATEGORIES AMONG THE MOST CONSTANT SPECIES AND AMONG THE TOTAL AND MEAN RECORDED FLORAS INSIDE AND OUTSIDE THE BIRD COLONIES

Plant Category	Species with 50% Frequency or Over					Total Recorded Flora							
						Aggregate Flora*					Means for Two Groups, Each of 10 Habitats		
	Birds		No Birds		Ratio	Birds		No Birds		Ratio	Birds	No Birds	Ratio
	(No.)	(%)	(No.)	(%)		(No.)	(%)	(No.)	(%)		(%)	(%)	
Introduced plants	6	19	3	6	3·2 : 1	46	28	65	21	1·3 : 1	22	14	1·6 : 1
Annuals and biennials	8	31	5	10	3·1 : 1	56	34	63	20	1·7 : 1	27	16	1.7 : 1
Succulents	11½	53	7½	15	3·5 : 1	22½	14	21½	7	2·0 : 1	36	10	3·8 : 1
Sclerophylls and switch plants	1	6	16½	34	1 : 5·7	18½	11	79½	26	1 : 2·3	8	30	1 : 3·7
Woody species	4	6	20	41	1 : 6·8	25	15	87	28	1 : 1·8	16	32	1 : 2·0
Heath species	0	0	11	22	(0 : 22)	1	0·6	82½	26	1 : 44·0	0·2	23	1 : 115·5

* Figures from amalgamated lists for two habitat groups.

Table 3 refers to the nine habitats with more than 10 per cent. of aliens in the recorded flora, and illustrates this affinity of annuals even more than aliens for the rookeries (see also Fig. 3). Average alien : annual ratios for these habitats were 1 : 1·34 in the six rookeries and 1 : 0·81 in the three control areas.

(*h*) *Characteristics of the Most Constant Species*

Tables 4 and 5 list the most constant species for areas with and without birds. Forty-eight species occur in 50 per cent. or more of the areas without birds, but only a third of this number in 50 per cent. or more of the bird colonies.

Table 6 summarizes the mean percentage frequencies of six plant categories in the total recorded floras of 10 rookeries and 10 other areas, and compares these with the percentage frequencies for the "dominants" (i.e. species of over 50 per cent. frequency). With the exception of succulents, the trends illustrated for the total floras in Figures 2 and 3 are reflected in magnified form by the dominant species, stressing the significance of the distribution pattern.

Aliens and annuals, both approximately 1½ times as common in the rookeries as outside them, are both more than three times as common when only the dominants are considered. The mean average for succulents in the bird flora is nearly four times greater than outside the rookeries, but, because the same species turn up fairly constantly in all the rookeries, the ratio drops to 2 : 1 when the amalgamated lists for rookeries and "non-rookeries" are compared. In the 50–100 per cent. frequency categories the ratio is again high (3·5 : 1).

Sclerophylls and switch plants, nearly four times as abundant away from the birds as among them when the means for the 20 habitats are considered, are over five times as abundant among the most constant species. Woody species have a rookery : "control area" ratio of *c*. 1 : 2 in the total and nearly 1 : 7 in the high frequency categories.

Ratios cannot be compared for heath species, as these are negligible in the rookery flora, but the percentages in the total and most constant flora unaffected by birds are not significantly different.

VIII. Relationship of Plant Life Form in Rookery, Dune, and Heath Vegetation

Only one of the 10 bird colonies investigated (viz. Gabo I.) occurs on dune sand, but the rookery vegetation generally is closer to that of dunes in many respects than it is to that of the normal "granite flora" undisturbed by birds.

The soils of the Wilson's Promontory control areas are grey sands closely resembling those of the bird colonies in appearance. The closer affinity of the rookery vegetation with that of the more mobile and less mature sand of the dunes is thought to be related to chemical factors, including soil reaction and the greater leaching of heath soils where there is no annual increment of guano or beach sand.

pH determinations made in the Mount Oberon control area on dunes and granite country showed the reaction of dune sand to lie between those of the coastal strip and the main coastal heath. Only where dune sand overlay the indigenous soil of the low granite cliff 2–3 m above beach level, was the surface found to be more alkaline than the soil at a depth of 10 cm; elsewhere it was more acid.

Air-dried samples from 2 and 10 cm on the dunes dropped from pH 6·5 and 7·0 on the scarcely modified beach sand of the inland face of the foredune to pH 6·0 and 6·5 on the more mature, brownish grey sand of the scrub-covered main dunes several hundred yards inland.

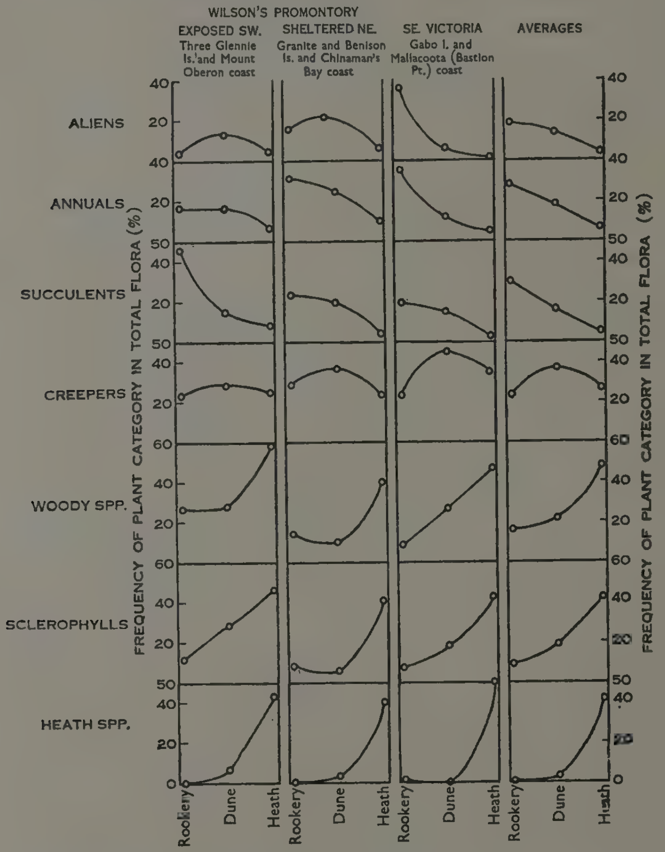

Fig. 4.—Distribution of seven bird categories in sea-bird rookeries overlying granite, sand dunes (no birds), and heath overlying granite (no birds). Averages (right-hand column) show intermediate position in dune vegetation of all plant categories except creeping plants, in spite of the physiographic differences of the substrate from that of the other two types of habitat.

The pH of the soil overlying granite dropped in a much shorter distance from 7·0 and 6·5, where subjected to blown salt spray and beach sand on the low cliff face, to 5·5 and 5·8 on the shingly, whitish, heavily leached soil of the coastal heath behind.

Dune vegetation as a whole was found to be intermediate, in respect of both life form and actual species, between that of rookeries and coastal heaths. Few species occur at all commonly in all three environments, and the most abundant, i.e. *Leptospermum laevigatum* and *Pteridium esculentum*, attain a maximum in the intermediate habitat. The majority of dune shrubs are restricted in the rookeries to the less heavily burrowed parts and in the heaths to the seaward fringes.

Typical heath species encroach further into the dune country than into the rookeries, and typical rookery species encroach further into the dune country than into the heath. Figures 2, 3, and 4 show the distribution trends of the various life forms considered in Appendix I, Figure 4 having special reference to the position of the various life forms in the three areas where dunes were investigated separately from the granite control area.

TABLE 7

DISTRIBUTION OF PLANT LIFE FORMS ETC. IN ROOKERY, DUNE, AND HEATH VEGETATION

Number of species in each category expressed as a percentage of the whole

Plant Category	Rookery	Dune	Heath	Range	Remarks
A. Maximum in rookeries:					Nutrients are being added to the soil
1. Introduced species	18	14	4	14	
2. Annuals and biennials	28	17	7	21	
3. Succulents	30	16	5	25	
B Maximum on the more mobile substrate of dunes:					Nutrients, except blown sea spray, not being added; but little leaching of existing nutrients
4. Creeping plants	23	37	29	14	
C. Maximum on heaths:					Marked leaching of soil nutrients has occurred
5. Woody plants	16	22	48	32	
6. Sclerophylls and switch plants	9	16	43	34	
7. Typical heath species	1	3	44	43	
D. No significant differences:					
8. Xeromorphic monocotyledons	9	6	8	3	

Sclerophylls, switch plants, and woody species show a tendency to increase from a minimum in the rookeries to a maximum in the heaths, with the dunes occupying an intermediate position.

Introduced plants, annuals and biennials, and succulent species show a tendency to decrease from a maximum in the rookeries to a minimum in the heaths, with the dunes again occupying an intermediate position. The large amount of bare sand unoccupied by perennials would assist the establishment on the dunes of the first three of these groups, and the fourth is well fitted to resist any possible summer soil drought.

Only in the case of creeping plants is the maximum seen to be on the dunes, this being related to the efficiency of this type of plant on the mobile substratum.

The number of species of xeromorphic monocotyledons is not significantly different in the three habitats, but the individuals cover more ground in rookeries and, to a lesser extent, on dunes than they do on heath. With increasing concentration of sea salt or guano this group—itself more "resistant" than the woody plants—is likely to give way to succulents—the most "resistant" of all the life forms present and often the only one to occur where high concentrations of guano and sea salt co-exist.

It is interesting to note in this connexion, therefore, that where rookery and dune are combined on Gabo I., it is a succulent which dominates the many acres of penguin colony on dune sand, although tussock grasses and shrubs dominate the dunes unoccupied by penguins, both on the island itself and on the adjacent mainland dunes near Mallacoota.

Average percentages for eight plant categories in rookery, dune, and heath in the three geographical zones graphed in Figure 4 are set out in Table 7. This indicates only the number of species concerned but reflects, in mitigated form, the area covered by each group in all cases except that of xeromorphic monocotyledons.

IX. Transition Zone of Plants with Intermediate Tolerances

The ecotone or transition from rookery vegetation to heathy dune scrub can be well seen at the margins of the Gabo I. rookery. The sequence of plants there is so similar to that around rookeries in southern and western Tasmania that it is possible to postulate certain species as typical of the transition zone. Conspicuous among these are plants of wide tolerance such as the *Leptospermum laevigatum* and *Pteridium esculentum* already mentioned in this connexion in the previous section on dunes.

These two species represent the commonest life forms in the transition from rookery to heath generally, but the Gabo I. area differs from the usual type in being situated largely on dune sand. Tussocky monocotyledons are of greater importance there than are shrubs, and form a belt with bracken between the *Carpobrotus* of the occupied dunes and the *Acacia/Banksia/Leptospermum* scrub of the unoccupied ones—effecting, in fact, a retreat of the various zones from the centre of occupation but keeping the order of these intact, viz. succulents–tussocks–bracken–coastal shrubs–heath species.

This arrangement is particularly obvious where "pockets" of penguin burrows only a few metres across occur away from the coast, and show a concentric zonation of progressively taller and "harsher" plants with increasing distance from the *Carpobrotus* around the burrows. With these inland colonies the transition is sharper than from the larger coastal ones where spray accentuates modifications caused by the birds. Tracks lead seawards between the bases of the tussocks and bracken fronds, and a few burrows are scattered among them. Where odd burrows occur beneath the shrubs of the outer zone, they are often accompanied by succulent growths of *Rhagodia baccata* which trail up through the branches.

Among the locally dominant plants of the transition zone are *Lomandra longifolia*, *Scirpus nodosus*, and *Poa poiformis* (all characteristic rookery species elsewhere), together with some *Sporobolus capensis* and *Ammophila arenaria*. Some of these tussocks penetrate the rookeries, whilst *Stenotaphrum secundatum* extends outwards from the rookery margins.

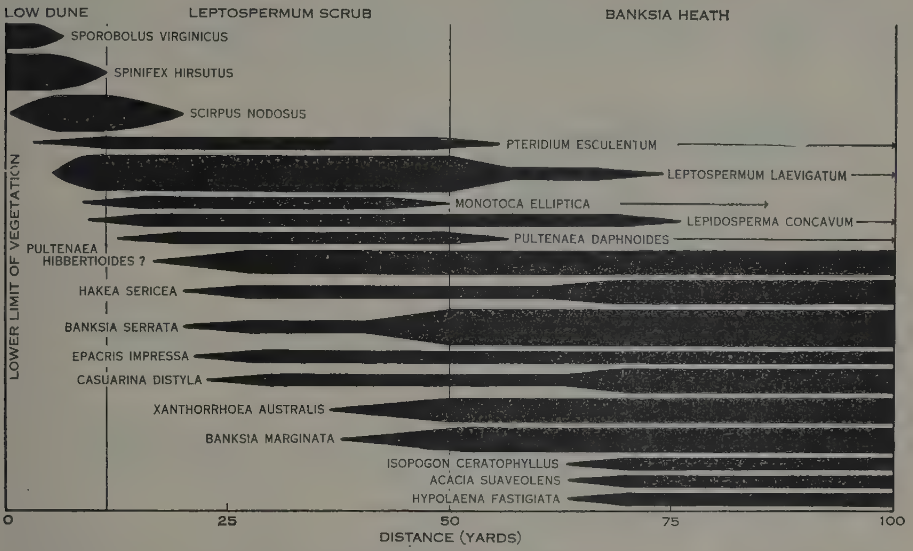

Fig. 5.—Relative abundance of the commoner species on Chinaman's Bay coast with increasing distance from the sea, 29.i.59, shown diagrammatically.

As in Tasmania, *Amperea spartioides* is one of the first of the heath species to come in as the *Carpobrotus* fades out at the rookery margins.

The following lists indicate the most characteristic plants of the burrowed, transition, and unburrowed zones on Gabo I., although the vegetation of the former zone is much simpler than that of the other two, often consisting solely of *Carpobrotus*, sometimes of only *Carpobrotus* and *Stenotaphrum*.

BURROWED ZONE

Carpobrotus rossii
Disphyma australe
Lepidosperma gladiatum
Lomandra longifolia
Muehlenbeckia adpressa
Poa poiformis
Pteridium esculentum
Rhagodia baccata
Scirpus nodosus
Senecio lautus
Solanum nigrum
Sporobolus capensis
Stenotaphrum secundatum
Tetragonia implexicoma
Zieria cytisoides

TRANSITION ZONE

Ammophila arenaria
Amperea spartioides
Dichelachne crinita
Dichondra repens
Holcus lanatus
Lepidosperma gladiatum
Leptospermum laevigatum
Lomandra longifolia
Oxalis corniculata
Poa poiformis
Pteridium esculentum
Rumex acetosella
Scirpus nodosus
Sporobolus capensis
Stenotaphrum secundatum

UNBURROWED ZONE

Acacia longifolia
A. suaveolens
Amperea spartioides
Astroloma humifusum
Banksia integrifolia
Epacris impressa
Halorrhagis tetragyna?
Helichrysum leucopsidum
Kennedya prostrata
K. rubicunda
Lepidosperma concavum
Leptospermum laevigatum
Monotoca elliptica
Olearia ramulosa
Persoonia juniperina

X. Parallel Effects of Guano and Sea Salt on Vegetation

Figure 5, illustrating the relative abundance of the commoner species with increasing distances from the Chinaman's Bay coast, shows a similar transition to that just described for the ecotone around the Gabo I. rookeries.

This is one of the most sheltered coasts examined, and the succulents which characteristically occupy soils of high base status are unimportant. The two most abundant species close to the coast are grasses, these leading to a narrow zone of *Scirpus nodosus* on the low embryo dunes. *Pteridium esculentum* occurs in the transition zone behind the beach with *Leptospermum laevigatum*, and dwindles to insignificant amounts about 50 m inland. The coastal belt of tea-tree scrub starts to thin out at about the same level, and yields place to open *Banksia serrata* heath with a high proportion of sclerophylls.

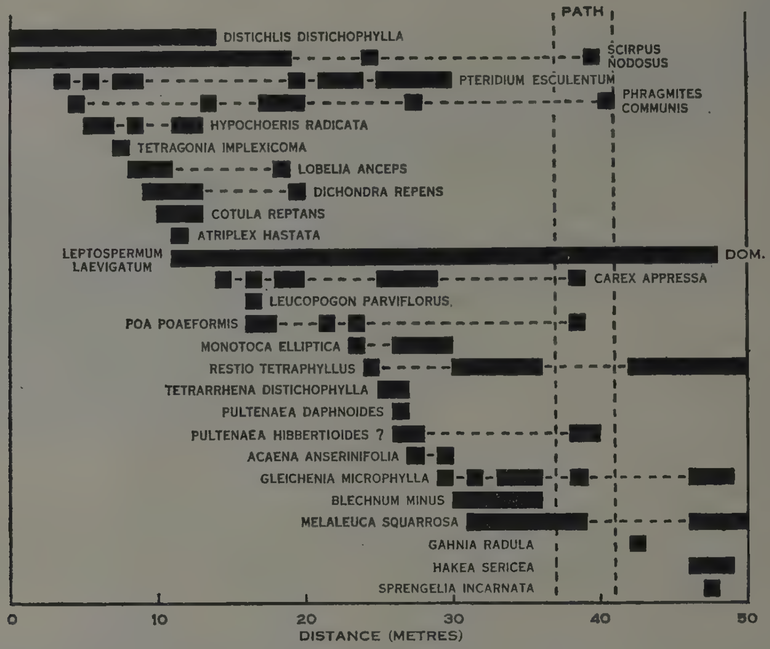

Fig. 6.—Transect 50 by 1 m, Chinaman's Bay, tea-tree scrub south of creek, 26.i.59. Range of species from seaward limit of vegetation 2–3 m south of creek bank is shown.

The relation to the general zonation postulated previously for rookeries is summarized in Table 8.

Figure 6 shows a more detailed version of the same type of coastal scrub, and includes all species in a strip 1 m broad south of the Chinaman's Bay Creek. Here the most seaward species is the grass, *Distichlis distichophylla*, followed by *Scirpus*, *Pteridium*, and *Leptospermum* as before, although there are no embryo dunes at this point.

The 10 species occurring to seaward of the *Leptospermum* are all herbaceous, four of them succulent or semisucculent. The 15 species appearing in the transect after the commencement of the *Leptospermum* zone include only eight herbs, none of them succulent, and seven shrubs.

On the adjacent Granite I. and Benison I. rookeries, succulents are conspicuous near the coast and the zones are pushed back, the more seaward broadened and the most inland excluded altogether. A summary of the general succession from the coast inland is given in Table 8.

TABLE 8

PLANT ZONATION FROM THE COAST INWARDS IN AREAS AFFECTED BY BIRDS AND AREAS NOT SO AFFECTED

Dominant Life Form of Zones from the Coast Inland	Granite and Benison Islands, Rookeries		Chinaman's Bay Coast, Control Area	
	Abundance	Chief Species	Abundance	Chief Species
(i) Succulents	Common	*Carpobrotus*, *Lepidium*, *Bulbine*, *Rhagodia*	—	—
(ii) Mesophytic herbs	Common	*Pelergonium*, *Senecio*, *Hypochoeris*	Sparse	*Spinifex*, *Sporobolus*, *Distichlis*
(iii) Tussocks	Common	*Poa*, *Stipa*, *Lomandra*	Sparse	*Scirpus*
(iv) Bracken	Medium	*Pteridium*	Medium	*Pteridium*
(v) Coastal shrubs	Medium	*Melaleuca*, *Acacia*, *Banksia integrifolia*	Common	*Leptospermum*, *Monotoca*
(vi) Heath	—	—	Common	*Banksia marginata*, *B. serrata*, *Casuarina*, *Hakea*, *Pultenaea*, *Xanthorrhoea*

The following represent more extreme examples of extension of the coastal plant zones in the rookeries:

(*a*) On Cliffy I. zone (i), represented by the succulent *Disphyma australe*, occupies almost the entire 100 acres. Zone (ii) is represented by *Lavatera arborea* and the alien herbs around the lighthouse, and zone (iii) by the 3 acres of *Poa poiformis* tussock on the island summit. Zones (iv) and (vi) are missing, and zone (v) is represented by a single clump of *Kunzea ambigua* a few metres across.

(*b*) On Citadel I. the succulents (*Disphyma* and the maritime form of *Senecio lautus*) again occupy most of the 70 acre island. Zones (ii) and (iii) are virtually excluded by the lack of soil, and zone (iv) by wind exposure. Zone (v) is fairly well represented by clumps of *Leptospermum laevigatum* and *Correa alba*, and zone (vi) is absent.

Separate analyses were made in the Mount Oberon district of three types of dune country and three types of granite country at increasing distances from the coast. The sequence of plant life forms from the coast inland on dunes matches that from the coastal granite strip to typical coastal heath, but is generally more gradual. In both sequences there is a marked decrease of succulents and creepers, a gradual decrease of aliens and annuals, and a marked increase of woody species, sclerophylls, and heath species. These differences are more clearly defined than on the Chinaman's Bay coast because of the greater exposure to the prevailing westerly winds.

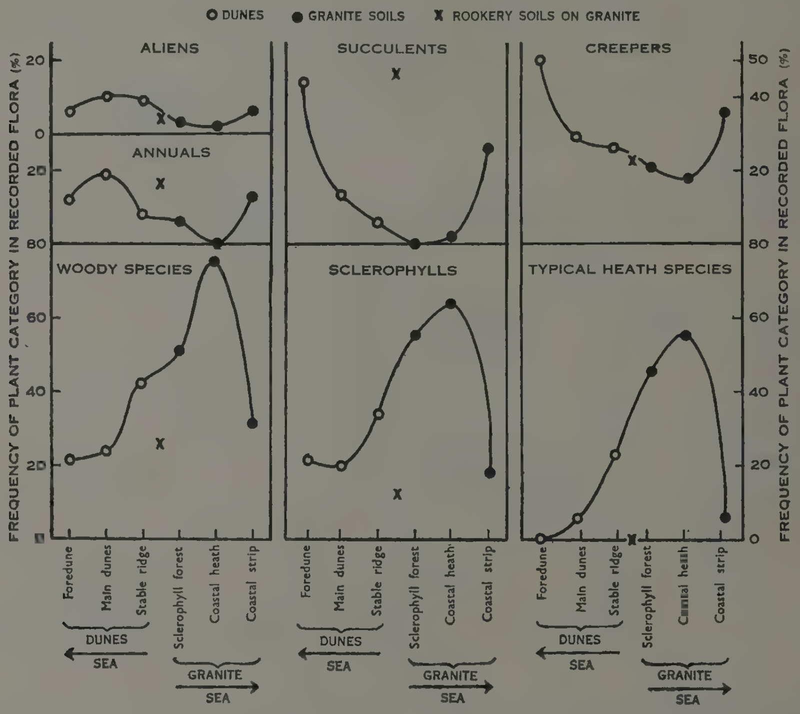

Fig. 7.—Distribution of seven plant categories in relation to proximity to the sea and type of substrate, Mount Oberon district, in the south-west of Wilson's Promontory.

The most inland granite habitat for which plants are listed is the mixed sclerophyll forest on the inner side of Mount Oberon; and the flora of this habitat was found to lie between that of the innermost of the dune systems and that of the more seaward coastal heath in the seven features referred to above. The herbs which flourish in the comparative protection of the forest and bring the percentage of woody species, sclerophylls, and heath species down are, however, different from those which grow on the coast where woody species are the more damaged by salt gales.

Percentage frequencies of the seven plant categories investigated are shown in Figure 7, which represents a circuit inland across the foredunes and main dunes of Oberon Bay, along a stable sand-ridge running at right angles to them as far as the central track to the lighthouse, through sclerophyll forest, and back seawards across coastal heath to the granite coast north of Growler's Creek.

In each of the seven graphs the coastal heath occupies the position on the curve furthest from that of the typical coast, sandy or rocky; i.e. it shows the highest proportion of woody, sclerophyllous, and heath species and the lowest of creepers, succulents, annuals, and aliens.

Apart from a narrow, discontinuous coastal strip of herbs, heath is the characteristic vegetation of coastal granite unoccupied by sea-birds. The characteristic vegetation of coastal granite occupied by sea-birds resembles a much magnified version of this discontinuous coastal strip. Hence the curves illustrate that the presence of nesting sea-birds can convert the flora from one extreme to the other, as far as the seven plant categories investigated in these six habitats are concerned.

XI. Acknowledgments

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APPENDIX I

LIST OF VASCULAR PLANTS, SHOWING DISTRIBUTION, STATUS, AND LIFE FORM

Nomenclature according to that in current use at the National Herbarium, Melbourne. Family order as in Ewart's "Flora of Victoria" (1930). Key to symbols in distribution table: H, determined at the National Herbarium. U, determined at the Melbourne University Botany Department. I, commonest in inland part of zone. (+), recorded on Doughboy I. in 1912 but not in 1959. M, species characteristic of but not necessarily confined to heath communities. Symbols in brackets have been accorded half unit value in the construction of totals

Species	Status		Longevity			Life Form						Habitat	Islands round Wilson's Promontory								Wilson's Promontory							South-eastern Victoria					Per Cent. Frequency	
	Native (N)	Introduced (I)	Annuals (A)	Biennials (B)	Perennials (P)	Creeping Plants (C)	Succulents (F)	Sclerophylls (X)	Switch Plants (S)	Xeromorphic Monocotyledons (Z)	Woody Species (W)	Typical Heath Species (M)	Citadel Island	Dannevig Island	McHugh Island	Cliffy Island	Rabbit Island	Granite Island	Benison Island	Doughboy Island	Oberon Bay Dunes	Oberon District Control	SE. Point Lighthouse Control	Three Mile Beach Control	Chinaman's Bay etc. Dunes	Chinaman's Bay etc. Control	Miller's Hut Coast Control	Gabo Island Rookery	Gabo Island Control Area	Mallacoota Bird Roost	Mallacoota Dunes	Mallacoota Control Area	Bird Colonies	Dunes and Control Areas
Selaginellaceae																																		
Selaginella uliginosa (Labill.) Spring (H)	N				P	C						M											U										—	10
Cyatheaceae																																		
Cyathea australis (R.Br.) Domin (H)	N				P						W									H													10	—
Polypodiaceae																																		
Lindsaya linearis Swartz	N				P	C						M																				+	—	10
Adiantum aethiopicum L.	N				P	C																										+	—	10
Pteridium esculentum (Forst. f.) Nakai	N				P	C		X									+	+	+	+	+	+	+	+	+	+	+	+	+		+	+	50	100
(*Pteris incisa* Thunb.)	N				P	C														(+)													10	—
Phymatodes diversifolia (Willd.) Pichi-Sermolli (H)	N				P	C														H													10	—
(*Polypodium pustulatum* (Forst. f.))	N				P	C														(+)													10	—
Blechnum minus (R.Br.) Ettingsh. (U)	N				P			X																		U			U				—	20
Asplenium flabellifolium Cav. (U)	N				P														U														10	—
A. obtusatum Forst. f. (U)	N				P		F						U		U	U												U	+				40	10
A. scleroprium? Homb. & Jacq.	N				P											+																	10	—
(*Aspidium aculeatum* Siv.)	N				P															(+)													10	—

Gleicheniaceae																														
Gleichenia circinnata Swartz (U)	N				P	C	X		M														U						—	10
G. microphylla R.Br. (U)	N				P	C	X		M												+		U						—	20
Typhaceae																														
Typha angustifolia L. (H)	N				P	C																		H					—	10
Potamogetonaceae																														
Zostera muelleri Irmisch ex Aschers (H)	N				P	C										H	+					+							20	10
Posidonia australis Hook. f.	N				P	C									+	+	+					+							30	10
Juncaginaceae																														
Triglochin procera R.Br. (U)	N				P	C												?					U						—	20
T. stricta Ruiz & Pav. (U)	N				P	C														+			U	+		+			—	40
Gramineae																														
Imperata cylindrica (L.) Pal. & Beauv.	N				P																			H		H			—	20
Themeda australis (R.Br.) Stapf	N				P																							+	—	10
Zoysia macrantha Desv. (H)	N				P	C																				H			—	10
Paspalum distichum L. (H)	N				P	C																				H			—	10
Stenotaphrum secundatum (Walt.) Kuntze		I			P	C														+					+	+			10	20
Pennisetum clandestinum Hochst. ex.		I			P	C																					H		—	10
Spinifex hirsutus Labill. (U)	N				P	C										+					U	+				+	+		10	40
Anthoxanthum odoratum L. (H)		I			P												H												10	—
Tetrarrhena distichophylla R.Br. (U)	N				P	C																	U				+	+	—	30
Microlaena stipoides (Labill.) R.Br. (H)	N				P	C											H									H		+	10	20
Distichlis distichophylla (Labill.) Fas.	N				P	C										+						+							10	10
Phragmites communis Trin. (U)	N				P	C																U	+	+		+			—	40
Dactylis glomerata L.		I			P																					+			—	10
Vulpia bromoides (L.) S. F. Gray (H)		I	A										+	+	+	H	H			+	+	+							50	30
Bromus diandrus Roth (H)		I	A	B									+		H	H		+		+					+				40	20
B. mollis L. (H)		I	A	B													H												10	—
B. unioloides (Willd.) Humb. *et al.*		I	A	B									+												+				20	—
Catapodium rigidum (L.) C. E. Hubbard		I			P												+	+							+	+			20	20
Briza maxima L.		I	A																	+									—	10
B. minor L.		I	A														+			+									10	10
Eragrostis brownii (Kunth) Nees ex Steud. (H)	N			B	P																					H			—	10
Poa annua L. (H)		I	A														H			+									10	10
P. australis agg.	N				P			Z									(+)		?				I						10	20
P. poiformis (Labill.) Druce (H)	N				P			Z		+	+	H	+	H	H	H	H			+	+	+		+	+	+			90	50
P. pratensis L.		I			P												+												10	—
Deyeuxia quadriseta (Labill.) Benth.	N				P																+		+		+	+			10	30
Agrostis avenacea J. F. Gmel. (U)	N				P												+			+	+	U	+	+	+	+			20	60
Dichelachne crinita (L.f.) Hook. f. (H)	N				P											+	H			+					+	+			30	20

APPENDIX I (*Continued*)

Species	Status		Longevity			Life Form						Habitat	Islands round Wilson's Promontory								Wilson's Promontory							South-eastern Victoria					Per Cent. Frequency	
	Native (N)	Introduced (I)	Annuals (A)	Biennials (B)	Perennials (P)	Creeping Plants (C)	Succulents (F)	Sclerophylls (X)	Switch Plants (S)	Xeromorphic Monocotyledons (Z)	Woody Species (W)	Typical Heath Species (M)	Citadel Island	Dannevig Island	McHugh Island	Cliffy Island	Rabbit Island	Granite Island	Benison Island	Doughboy Island	Oberon Bay Dunes	Oberon District Control	SE. Point Lighthouse Control	Three Mile Beach Control	Chinaman's Bay etc. Dunes	Chinaman's Bay etc. Control	Miller's Hut Coast Control	Gabo Island Rookery	Gabo Island Control Area	Mallacoota Bird Roost	Mallacoota Dunes	Mallacoota Control Area	Bird Colonies	Dunes and Control Areas
Gramineae (*Continued*)																																		
(*Dichelachne sciurea* (R.Br.) Hook. f.)	N				P															(+)													10	—
Lagurus ovatus L.		I	A	B												+							+										10	10
Stipa compacta D. K. Hughes	N				P																								+				—	10
S. eremophila F. M. Reader (U)	N				P																				U								—	10
S. teretifolia Steud. (U)	N				P					Z				+					+			+	+	+	U	+	+	+	+				30	70
Ammophila arenaria (L.) Link (U)		I			P	C				Z							+							U	U			+	+				20	30
Sporobolus capensis Kunth (H)	N				P																							H	+		+		10	20
S. virginicus (L.) Kunth (U)	N				P	C																			U								—	10
Eleusine indica (L.) J. Gaertn.?		I			P	C																							+				—	10
Cynodon dactylon (L.) Pers. (H)		I			P	C										H																	10	—
Holcus lanatus L.		I			P														+	+			+		+			+	+				30	30
Aira caryophyllea L. (U)		I	A																+	+	+		+		U	+	+	+	+				30	60
A. praecox L. (H)		I	A																+	H					+	+							20	20
Danthonia caespitosa Gaudich. (H)	N				P					Z			H																				10	—
D. racemosa R.Br. (H)	N				P					Z										H													10	—
D. setacea R.Br. (U)	N				P					Z		M												+	+	U							—	30
D. sp.	N				P					Z													+									+	—	20
Lolium perenne L.		I			P											+							+						+				10	20
Monerma cylindrica (Willd.) Coss. & Durieu	N		A																									+	+				10	10
Parapholis incurva (L.) C. E. Hubbard	N		A													+				+			+		+								20	20
Agropyron junceiforme (A. & D. Löve) A. & D. Löve (H)		I			P	C															H												—	10
A. scabrum (Labill.) Pal. Beauv.	N				P															+													10	—
Hordeum leporinum Link?		I	A													+							+										10	10

Cyperaceae																							
Scirpus antarcticus L. (H)	N		P						H	+						+						20	10
S. cernuus Vahl (H)	N	A							+	H	H?					H	+	+	+			30	40
S. inundatus (R.Br.) Poir. (H)	N		P													H	+					—	20
S. nodosus Rottb. (U)	N		P	C	Z			+	+	+	+	+	+	U	+	+	+	+	+	+		40	90
Carex appressa R.Br. (H)	N		P													H						—	10
C. sp.	N		P								+					+			+			—	30
Gymnoschoenus sphaerocephalus (R.Br.) Hook. f.	N		P		Z	M								I								—	10
Schoenus apogon Roem. & Schult. (H)	N		P	C?		M?															H	—	10
S. brevifolius R.Br. (H)	N		P	C		M?															H	—	10
S. nitens (R.Br.) Poir. (H)	N		P	C								+	H									—	20
Cladium acutum (Labill.) Poir. (H)	N		P	C?	Z	M							H									—	10
C. junceum R.Br. (H)	N		P	C	Z	M							H									—	10
Lepidosperma concavum R.Br.	N		P	C	Z	M						+	I	I		+	+		+		+	—	70
L. elatius Labill. var. *ensiforme* Rodway (H)	N		P	C?	Z							H										—	10
L. gladiatum Labill.	N		P	C	Z						+	+	+		+		+	+		+		10	60
L. neesii Kunth (H)?	N		P	C?	Z	M															H	—	10
Gahnia radula (R.Br.) Benth. (H)	N		P	C?	Z							?							H		+	—	30
G. trifida Labill. (H)	N		P	C?	Z												H					—	10
Araceae																							
Zantedeschia aethiopica (L.) Spreng.	I		P							+			+									10	10
Restionaceae																							
Restio tetraphyllus Labill.	N		P	C		M										+						—	10
Leptocarpus brownii Hook. f. (H)	N		P	C	Z								H			H	+		+			—	40
Hypolaena fastigiata R.Br.	N		P		Z	M							+	I			+					—	30
Calorophus lateriflorus (R.Br.) F. Muell. (H)	N		P		Z	M								I		+						—	20
Centrolepidaceae																							
Centrolepis fascicularis Labill.?	N	A				M								+		+						—	20
C. strigosa (R.Br.) Roem. & Schult. (H)	N	A							H				+		+	+	+		+			10	50
Xyridaceae																							
Xyris gracilis R.Br.?	N		P			M								I								—	10
Juncaceae																							
Luzula campestris (L.) DC. (H)	N		P						H	H				+		+						20	20
Juncus articulatus L. (H)	N		P													H						—	10
J. bufonius L. (H)	N	A					+		H	+				+	+	+						30	30
J. caespiticius E. Mey. (H)	N		P										H			H	?		+			—	40
(*J. communis*)	N		P							(+)												10	—
J. maritimus Lam. (H)	N		P	C					+				+				H		+			10	30
J. pallidus R.Br. (H)	N		P						+	H			+				+	+	+	+		30	40

APPENDIX I (*Continued*)

Species	Status		Longevity			Life Form						Habitat	Islands round Wilson's Promontory								Wilson's Promontory							South-eastern Victoria					Per Cent. Frequency	
	Native (N)	Introduced (I)	Annuals (A)	Biennials (B)	Perennials (P)	Creeping Plants (C)	Succulents (F)	Sclerophylls (X)	Switch Plants (S)	Xeromorphic Monocotyledons (Z)	Woody Species (W)	Typical Heath Species (M)	Citadel Island	Dannevig Island	McHugh Island	Cliffy Island	Rabbit Island	Granite Island	Benison Island	Doughboy Island	Oberon Bay Dunes	Oberon District Control	SE. Point Lighthouse Control	Three Mile Beach Control	Chinaman's Bay etc. Dunes	Chinaman's Bay etc. Control	Miller's Hut Coast Control	Gabo Island Rookery	Gabo Island Control Area	Mallacoota Bird Roost	Mallacoota Dunes	Mallacoota Control Area	Bird Colonies	Dunes and Control Areas
Liliaceae																																		
Xanthorrhoea australis R.Br. (U)	N				P					Z	W	M										+	I	I		UI	I						—	60
Lomandra longifolia Labill. (U)	N				P					Z									+				+	U	+		+	+	+				20	50
Dianella revoluta R.Br.	N				P					Z							+			+	+				+	+		+	+				30	30
Anguillaria dioica R.Br. (H)	N				P							M?									H												—	10
Bulbine semibarbata (R.Br.) Haw.	N				P		F							+	+	+	+	+		(+)													60	—
Commelinaceae																																		
Tradescantia fluminensis Vell. (H)		I			P	C																	H										—	10
Orchidaceae																																		
Dipodium punctatum (Sm.) R.Br. (U)	N				P				S			M														UI							—	10
Thelymitra sp.? (H)	N				P							M																	H				—	10
Microtis unifolia (Forst. f.) Reichenb. f.	N				P														+				+										10	10
Acianthus reniformis (R.Br.) Schlechtendal (H)	N				P																H												—	10
Pterostylis sp. (U)	N				P							M														UI							—	10
Casuarinaceae																																		
Casuarina distyla Vent. (U)	N				P				S		W	M										+		I		UI	I					+	—	50
C. stricta Dryand (H)	N				P				S		W										H	+	H?	+			+						—	50
Urticaceae																																		
Ficus carica (H) L.		I			P																								H				—	10
Urtica dioica L.		I			P	C																								+			10	—
U. incisa Poir.	N				P															+													10	—
Parietaria debilis Forst. f.	N		A	B	P															+													10	—

Proteaceae																															
Persoonia juniperina Labill. (H)	N			P			X	W	M										+					+		H				—	30
Isopogon ceratophyllus R.Br. (U)	N			P			X	W	M										+	I	I		U							—	40
Banksia integrifolia L.f. (H)	N			P			X	W								H	+	+	+		+			+	H	+		+	+	30	70
B. marginata Cav. (U)	N			P			X	W	M										+	+	U	+	U			+			+	—	70
B. serrata L.f. (U)	N			P			X	W	M												U		U	+						—	30
Lomatia ilicifolia R.Br. (H)	N			P			X	W	M																	+			H	—	20
Hakea rostrata F. Muell. ex Meissn.? (U)	N			P			X	W	M														U							—	10
H. sericea Schrad. & J. Wendl. (H)	N			P			X	W	M									+	+	H			+							—	40
H. teretifolia (Salisb.) J. Britt. (H)	N			P			X	W	M																				H	—	10
H. ulicina R.Br. (H)	N			P			X	W	M										H											—	10
Grevillea lanigera A. Cunn. ex R.Br. (U)	N			P			X	W	M										+				U							—	20
Polygonaceae																															
Polygonum aviculare L. agg.		I	A		C															+										—	10
P. minus Huds. (H)		I	A																							H				—	10
Muehlenbeckia adpressa (Labill.) Meissn.	N			P	C			W						+		+			+		+	+			+	+	+	+	+	40	60
Rumex acetosella L.		I		P	C													+						+		+				—	30
R. brownii Campd. (H)	N			P													H					+			+	+				20	20
R. crispus L. (H)		I		P									+												H	+				20	10
Chenopodiaceae																															
Atriplex cinerea Poir.	N			P		F		W													+									—	10
A. hastata L.		I	A			(F)							+	+		+	+					+			+					50	10
Rhagodia baccata (Labill.) Moq. (U)	N			P		F		W			+	+			+			+			+	+	U		+					40	40
Chenopodium glaucum L. (H)	N		A			F											H					+			+					20	10
C. murale L.		I	A										+							+										10	10
C. trigonum Schult. (H)	N		A?																						H					10	—
Salicornia australis Soland. ex Benth. (H)	N			P		F					+		+			H	H					+		+						40	20
Hemichroa pentandra R.Br. (H)	N			P	C	F										H						+								10	10
Phytolaccaceae																															
Phytolacca octandra L.		I		P		(F)																					+			10	—
Aizoaceae																															
Disphyma australe (Soland.) J. M. Black	N			P	C	F				+	+	+	+	+		+									+	+				70	10
Carpobrotus rossii (Haw.) N.E.Br. (U)	N			P	C	F					+	+		+	+	+	(+)	+	+	+	U	+			+	+	+	+		80	70
Tetragonia implexicoma (Miq.) Hook. f.	N			P	C	F					+	+				+		+		+	+	+			+		+	+		50	50
T. tetragonioides (Pallas) O. Kuntze	N			P	C	F																+								—	10
Portulacaceae																															
Portulaca oleracea L. (H)	N		A		C	F							+													H				10	10
Calandrinia calyptrata Hook. f.	N		A		C	F					+	+	+	+			(+)													50	—

APPENDIX I (*Continued*)

Species	Status		Longevity			Life Form						Habitat	Islands round Wilson's Promontory								Wilson's Promontory							South-eastern Victoria					Per Cent. Frequency	
	Native (N)	Introduced (I)	Annuals (A)	Biennials (B)	Perennials (P)	Creeping Plants (C)	Succulents (F)	Sclerophylls (X)	Switch Plants (S)	Xeromorphic Monocotyledons (Z)	Woody Species (W)	Typical Heath Species (M)	Citadel Island	Dannevig Island	McHugh Island	Cliffy Island	Rabbit Island	Granite Island	Benison Island	Doughboy Island	Oberon Bay Dunes	Oberon District Control	SE. Point Lighthouse Control	Three Mile Beach Control	Chinaman's Bay etc. Dunes	Chinaman's Bay etc. Control	Miller's Hut Coast Control	Gabo Island Rookery	Gabo Island Control Area	Mallacoota Bird Roost	Mallacoota Dunes	Mallacoota Control Area	Bird Colonies	Dunes and Control Areas
Caryophyllaceae																																		
Stellaria media (L.) Cyrillo		I	A														+						+					+	+				20	20
S. multiflora Hook. (H)	N		A																H														10	—
Cerastium glomeratum Thuill.		I	A																+	+	+	+	+				+						20	40
Moenchia erecta (L.) P. Gaertn. *et al.*		I	A																					+									—	10
Sagina apetala L.	N		A													+			+	+													30	—
S. procumbens L.	N				P																+							+	+				10	20
Spergularia media (L.) C. Presl.	N				P		F									+	+																20	—
Polycarpon tetraphyllum (L.) Loefl.		I	A													+				+			+		+	+	+						20	40
Silene gallica L.		I	A																				+					+	+				10	20
Ranunculaceae																																		
Clematis aristata R.Br. ex DC.	N				P	C														+													10	—
C. microphylla DC.	N				P	C													+		+										+	+	10	30
Lauraceae																																		
Cassytha glabella R.Br.? (H)	N				P	C			S			M																				H	—	10
C. pubescens R.Br.?	N				P	C			S			M														+							—	10
Fumariaceae																																		
Fumaria officinalis L.		I	A													+							+										10	10
Cruciferae																																		
Nasturtium officinale R.Br.		I			P	C																							+				—	10
Sisymbrium orientale L.		I	A	B																			+										—	10

Lepidium foliosum Desv. (H)	N				P		F								H														10	—
L. praetervisum Domin (H)	N		A	B																H									—	10
Raphanus raphanistrum L. (H)		I	A	B																H									—	10
Cakile maritima Scop. (H)	N		A				F												H										—	10
C. maritima var. *edentula* (Hook.) Jord.	N		A				F							+		+											+		20	10
Droseraceae																														
Drosera binata Labill. (U)	N				P					M													U						—	10
D. planchoni Hook. f.	N				P					M										+									—	10
D. pygmaea DC. (U)	N				P					M											+				U				—	20
Crassulaceae																														
Crassula sieberiana (Schult. & Schult. f.) Druce (H?)	N		A				F				+	+	+	+	+	+	+	H?		+	+			+	+	+			70	50
Pittosporaceae																														
Billardieri scandens Sm. (U)	N				P	C		X	W	M													U			+			—	20
(*Pittosporum undulatum* Vent.)	N				P			X	W								(+)												10	—
Bursaria spinosa Cav.	N				P				W									+		+									—	20
Rosaceae																														
Rubus fruticosus L. agg.		I			P	C			W										+							+			—	20
Acaena anserinifolia (Forst. & Forst. f.) Druce	N				P	C										+	+	+	+	+	?	+	+		+	+	+	+	30	90
Mimosaceae																														
Acacia botrycephala (Vent.) Desf. (H)	N				P				W																			H	—	10
A. longifolia (Andr.) Willd. (H)	N				P			X	W					H					H									H?	10	15
A. longifolia var. *sophorae* (Labill.) F. Muell. (H)	N				P			X	W						+			+			+	+	+	+		+	H	+	10	90
A. melanoxylon R.Br. (H)	N				P			X	W							H	(+)											+	20	10
A. mucronata Willd.? (H)	N				P			X	W									?										H?	—	15
A. stricta (Andr.) W lld. (H)	N				P			X	W			H								H									10	10
A. suaveolens (Sm.) Willd.	N				P			X	W	M									H				+	+		H		H	—	50
A. verticillata (L'Hér.) Willd. var. *latifolia* DC.	N				P			X	W									+	+	+				+					—	40
Albizia lopantha (Willd.) Benth. (H)	N				P				W								H												10	—
Papilionaceae																														
Daviesia ulicina Andr. (H)	N				P			X	W	M										H									—	10
D. ulicina var. *ruscifolia* (A. Cunn. ex Benth.) Benth. (H)	N				P			X	W	M									H										—	10
Pultenaea daphnoides J. Wendl. (U)	N				P			X	W	M									+	I	I		U						—	40
P. hibbertioides Hook. f.? (U)	N				P			X	W	M											I		UI	?					—	30
P. retusa Sm. (H)	N				P			X	W	M									?							H		+	—	30

APPENDIX I (*Continued*)

Species	Status		Longevity			Life Form						Habitat	Islands round Wilson's Promontory								Wilson's Promontory							South-eastern Victoria					Per Cent. Frequency	
	Native (N)	Introduced (I)	Annuals (A)	Biennials (B)	Perennials (P)	Creeping Plants (C)	Succulents (F)	Sclerophylls (X)	Switch Plants (S)	Xeromorphic Monocotyledons (Z)	Woody Species (W)	Typical Heath Species (M)	Citadel Island	Dannevig Island	McHugh Island	Cliffy Island	Rabbit Island	Granite Island	Benison Island	Doughboy Island	Oberon Bay Dunes	Oberon District Control	SE. Point Lighthouse Control	Three Mile Beach Control	Chinaman's Bay etc. Dunes	Chinaman's Bay etc. Control	Miller's Hut Coast Control	Gabo Island Rookery	Gabo Island Control Area	Mallacoota Bird Roost	Mallacoota Dunes	Mallacoota Control Area	Bird Colonies	Dunes and Control Areas
Papilionaceae (*Continued*)																																		
P. stricta Sims. (H)	N				P			X			W	M														H							—	10
Dillwynia glaberrima Sm. (H)	N				P			X			W	M									+	H							H			+	—	40
Lotus corniculatus L. (H)		I			P	C																							H				—	10
Trifolium campestre Schreb.		I	A																										+				—	10
T. dubium Sibth.		I	A																				+						+				—	20
T. repens L.		I			P	C																	+				+		+				—	30
Medicago arabica (L.) All.		I	A																				+										—	10
M. hispida J. Gaertn. var. *denticulata* (Willd.) Burnat (H)		I	A																										H				—	10
Platylobium obtusangulum Hook.	N				P			X			W	M														I							—	10
Bossiaea cinerea R.Br.	N				P			X			W	M														I							—	10
Swainsonia lessertifolia DC.	N				P	C															+	+									+		—	30
Glycine clandestina J. Wendl. (H)	N				P	C																							H		H	+	—	30
Kennedya prostrata R.Br.	N				P	C						M										+				+			+			+	—	40
K. rubicunda (Schneev.) Vent. (H)	N				P	C																							H				—	10
Geraniaceae																																		
Pelargonium australe Willd.	N				P									+	+	+		+	+	(+)	+			+	+						+		60	40
Geranium dissectum L.		I			P															+													10	—
G. molle L.		I	A																				+				+						—	20
G. pilosum Forst. f. ex Willd.	N				P																+						+						—	20
Erodium cicutarium (L.) Ait.		I	A	B																								+	+				10	10

Oxalidaceae																																	
Oxalis corniculata L.	N				P	C													(+)	+		+	+	+	+	+			+		+	20	70
Rutaceae																																	
Correa alba Andr. (H)	N				P					W		+	+	+		H		H	H	+	H		+	+	+			+		+		60	70
C. reflexa (Labill.) Vent. (H)	N				P					W	M										+	H			+	I					+	—	50
Zieria cytisoides Sm. (H)	N				P					W																	H	+				10	10
Tremandraceae																																	
Tetratheca ciliata Lindl.	N				P			X		(W)	M?										+											—	10
Polygalaceae																																	
Comesperma volubile Labill. (H)	N				P	C					M																	H				—	10
Euphorbiaceae																																	
Euphorbia peplus L.		I	A																+													10	—
Poranthera microphylla Brongn. (U)	N		A																(+)						U							10	10
Amperea (spartioides) = xiphoclada (Sieb. ex Spreng.) Druce (U)	N				P			(X)	(S)	W	M										+	I	I		U		+	+				10	50
Stackhousiaceae																																	
Stackhousia spathulata Sieb. ex Spreng. (H)	N				P		F													H												—	10
S. viminea Sm. (U)	N				P						M												UI									—	10
Rhamnaceae																																	
Pomaderris apetala Labill.	N				P					W													+									—	10
P. oraria F. Muell. ex Reiss. (H)	N				P					W	M?										H											—	10
Spyridium parvifolium (Hook.) F. Muell. (H)	N				P					W										+	+	H	+									—	40
S. cinereum N. A. Wakefield (H)	N				P					W	M?																				H	—	10
Malvaceae																																	
Hibiscus trionum L. (H)		I	A																									H				—	10
Lavatera plebeja Sims.	N		A	B	P								+	+	+		+		+													50	—
Malva parviflora L.?		I	A			C									+							+						+				10	20
Modiola caroliniana (L.) G. Don		I	A	B	P	C																+										—	10
Dilleniaceae																																	
Hibbertia acicularis (Labill.) F. Muell. (H)	N				P	C		X		W	M												+								H	—	20
H. aff. *aspera* DC. (H)	N				P			X		W	M																				H	—	10
H. asterotricha Sieber. ex Spreng. (H)	N				P			X		W	M												?								H	—	20
H. sericea (R.Br. ex DC.) Benth. (H)	N				P			X		W	M									H	+										?	—	30
Guttiferae																																	
Hypericum gramineum Forst. f. (H)	N				P						M																				H	—	10

APPENDIX I (*Continued*)

Species	Status		Longevity			Life Form						Habitat	Islands round Wilson's Promontory								Wilson's Promontory							South-eastern Victoria					Per Cent. Frequency	
	Native (N)	Introduced (I)	Annuals (A)	Biennials (B)	Perennials (P)	Creeping Plants (C)	Succulents (F)	Sclerophylls (X)	Switch Plants (S)	Xeromorphic Monocotyledons (Z)	Woody Species (W)	Typical Heath Species (M)	Citadel Island	Dannevig Island	McHugh Island	Cliffy Island	Rabbit Island	Granite Island	Benison Island	Doughboy Island	Oberon Bay Dunes	Oberon District Control	SE. Point Lighthouse Control	Three Mile Beach Control	Chinaman's Bay etc. Dunes	Chinaman's Bay etc. Control	Miller's Hut Coast Control	Gabo Island Rookery	Gabo Island Control Area	Mallacoota Bird Roost	Mallacoota Dunes	Mallacoota Control Area	Bird Colonies	Dunes and Control Areas
Violaceae																																		
Viola hederaceae Labill.	N				P	C																+	+	+	+	+	+		+			+	—	80
Thymelaeaceae																																		
Pimelea sp.	N				P						W												+	+							+		—	30
Myrtaceae																																		
Eucalyptus baxteri (Benth.) Maiden & Blakely? (H)	N				P			X			W	M										H											—	10
E. globulus Labill. (H)	N				P			X			W	M											H										—	10
E. gummifera (J. Gaertn.) Mochr. (H)	N				P			X			W	M?																				H	—	10
E. obliqua L'Hér. (H)	N				P			X			W	M										H					I						—	20
(*E. paludosa* R. T. Baker) (leaves only))	N				P			X			W	M								(+)													10	—
E. viminalis Labill. (fls. & frs.)	N				P			X			W									+													10	—
E. sp. (peppermint group) (H)	N				P			X			W																H						—	10
Angophora floribunda (Sm.) Sweet (H)	N				P			X			W	M?																				H	—	10
Leptospermum laevigatum (J. Gaertn.) F. Muell. (H)	N				P			X			W		+		H						+	H	+	+	+	+		+	+		+	+	30	90
L. juniperinum Sm. (H)	N				P			X			W	M										+	H			I	H					H	—	50
L. myrsinoides Schlechtendal	N				P			X			W	M												I		I							—	20
L. sp.	N				P			X			W									+													10	—
Melaleuca ericifolia Sm. (H)	N				P			X			W								H	H			+			+	+		+		+	+	20	60
M. squarrosa Donn. ex Sm. (U)	N				P			X			W	M										+		I		U							—	30
Kunzea ambigua (Sm.) Druce (H)	N				P			X			W					+						+	H			+							10	30

Onagraceae																													
Epilobium billardierianum Ser. ex DC. (H)	N				P												+			+		+			H			—	40
E. junceum Forst. f. ex Spreng. (H)	N				P	C?									H	H												20	—
Haloragaceae																													
Haloragis tetragyna (Labill.) Hook. f.?	N				P	C		X		M								+	+			+	I		+		+	—	60
Myriophyllum amphibium Labill. (H)	N				P	C				(M)									H									—	10
Umbelliferae																													
Centenalla asiatica (L.) Urban (H)	N				P	C													H		+	H			+			—	40
Hydrocotyle hirta R.Br. ex A.Rich. f. (H)	N				P	C										(+)						H?	?					10	20
H. peduncularis R.Br. ex A.Rich. (H)	N		A	B	P	C											+		H	+		+			?	+	+	—	70
Apium prostratum Labill. (normal form) (H)	N				P	C	F						H		+		+	+		+	+		+	+	+	+		20	70
(*A. prostratum* Labill. (large form) (H))	N				P	C	F				H	H	H															30	—
(*A. graveolens* (U))		I	B								U	U	U															30	—
Petroselinum crispum (Mill.) auct. anon. (H)		I		B															H									—	10
Epacridaceae																													
Epacris impressa Labill. (U)	N				P			X	W	M							+	+	I	I		UI	I		+		+	—	80
Sprengelia incarnata Sm. (U)	N				P			X	W	M								+				UI						—	20
Acrotriche serrulata (Labill.) R.Br. (H)	N				P			X	W	M									H									—	10
Monotoca elliptica (Sm.) R.Br. (U)	N				P			X	W								+	+	+	+		U			+		+	—	70
Astroloma humifusum (Cav.) R.Br. (U)	N				P			X	W	M								+	+			U			+		+	—	50
Leucopogon ericoides (Sm.) R.Br. (H)	N				P			X	W	M								H										—	10
L. parviflorus (Andr.) Lindl. (H)	N				P			X	W						+	H	+	+	+	U		U	+					20	60
L. virgatus (Labill.) R.Br. (U)	N				P			X	W	M												UI						—	10
Cyathodes juniperina (Forst. & Forst. f.) Druce (H)	N				P			X	W					H		(+)						+						20	10
Primulaceae																													
Anagallis arvensis L.		I	A										+			+	+	+	+		+	+	+			+	+	20	80
Samolus repens (Forst. & Forst. f.) Pers.	N				P	C															+		+		+			—	30
Loganiaceae																													
Mitrasacme pilosa Labill. (H)	N				P					M												H						—	10
Gentianaceae																													
Centaurium pulchellum (Sw.) Krause	N		A												+	+	+	+	+	+	+		+				+	20	70
Apocynaceae																													
Alyxia buxifolia R.Br. (U)	N				P			X	W		+						+	+				U						10	30
Vinca major L.		I			P	C										+												10	—
Convolvulaceae																													
Dichondra repens Forst. & Forst. f. (H)	N				P	C									H	+	+	+	+	+	+	+	+	+	+	+		30	90

APPENDIX I (*Continued*)

Species	Status		Longevity			Life Form						Habitat	Islands round Wilson's Promontory								Wilson's Promontory							South-eastern Victoria					Per Cent. Frequency	
	Native (N)	Introduced (I)	Annuals (A)	Biennials (B)	Perennials (P)	Creeping Plants (C)	Succulents (F)	Sclerophylls (X)	Switch Plants (S)	Xeromorphic Monocotyledons (Z)	Woody Species (W)	Typical Heath Species (M)	Citadel Island	Dannevig Island	McHugh Island	Cliffy Island	Rabbit Island	Granite Island	Benison Island	Doughboy Island	Oberon Bay Dunes	Oberon District Control	SE. Point Lighthouse Control	Three Mile Beach Control	Chinaman's Bay etc. Dunes	Chinaman's Bay etc. Control	Miller's Hut Coast Control	Gabo Island Rookery	Gabo Island Control Area	Mallacoota Bird Roost	Mallacoota Dunes	Mallacoota Control Area	Bird Colonies	Dunes and Control Areas
Verbenaceae																																		
Avicennia marina (Forsk.) Vierh. var. *resinifera* (Forst.) Bakh.	N				P			X			W																+						—	10
Labiatae																																		
Mantha gracilis R.Br. var. *serpyllifolium* (Benth.) Ewart	N				P?																				+								—	10
M. spicata L. (H)		I			P																								H				—	10
Solanaceae																																		
Lycium ferocissimum Miers		I			P						W																		+				—	10
Physalis peruviana L.		I			P																								+				—	10
Solanum aviculare Forst. f. (H)	N				P						W									H						+			+		+	+	10	40
S. nigrum L. (H)	N		A	B																(+)							+	+	+	H			30	20
Scrophulariaceae																																		
Cymbalaria muralis P. Gaertn. *et al.*		I			P	C																	+										—	10
Veronica plebeja R.Br. (H)	N				P	C						M																				H	—	10
Myoporaceae																																		
Myoporum insulare R.Br. (H)	N				P		(F)	(X)			W									H		+		U		U			+			+	10	50
Plantaginaceae																																		
Plantago coronopus L.		I	A	B												+							+		+		+	+	+	+			30	40
P. lanceolata L.		I			P																		+						+	+			10	20

Plantago major L.		I		P															+							+		—	20
P. varia R.Br.	N			P																						+		—	10
Rubiaceae																													
Opercularia ovata Hook. f. (H)	N			P			X		M																	H	H?	—	20
Galium aparine L.		I	A		C		X													+								—	10
G. australe DC.	N			P	C		X													+								—	10
G. propinquum A. Cunn. (H)	N			P			X									+											H	10	10
Caprifoliaceae																													
Sambucus sp.	N			P				W				+		+	+	+		+										40	10
Campanulaceae																													
Wahlenbergia billardieri N. Lothian (H)	N			P					(M)																		H	—	10
W. gracilis (Forst.) Alph. DC. agg.	N			P															+		+	+						—	30
W. gymnoclada N. Lothian (H)	N			P					(M)																		H	—	10
W. quadrifida (R.Br.) Alph. DC.? (H)	N			P											H													10	—
W. tadgellii? N. Lothian? (H)	N			P												H												10	—
Lobeliaceae																													
Lobelia anceps L. f.	N			P	C	F				+	+		+	+	+	(+)		+	+	+	+	+	+	+	+			70	70
Goodeniaceae																													
Goodenia ovata Sm. (U)	N			P				(W)	(M)									+	+			U					+	—	40
Selliera radicans Cav. (H)	N			P	C	F									H	(+)		+	+		+		+		+			20	50
Scaevola sp.	N			P		F															+							—	10
Dampiera stricta (Sm.) R.Br. (U)	N			P			X		M													U						—	10
Stylidiaceae																													
Stylidium graminifolium Swartz (H)	N			P			X		M								H		+									—	20
Compositae																													
Lagenophora stipitata (Labill.) Druce (H)	N			P																		H					+	—	20
Brachycome diversifolia (R. Graham ex Hook.) Fisch. & C. Mey. var. *maritima* Benth. (H)	N			P							H																	10	—
B. graminea (Labill.) F.Muell. (H)	N			P	C												?									H		—	20
Erigeron bonariensis L. (H)		I	A																					H	H	+		20	10
E. canadenses L. ?		I	A																						+	+		10	10
Olearia axillaris (DC.) Benth.	N			P				W													+	+						—	20
O. phlogopappa (Labill.) DC. (H)	N			P				W				H							+									10	10
O. ramulosa (Labill.) Benth. (H)	N			P			X	W	M																	H		—	10
O. rugosa (F. Muell. ex Archer) Hutch. (H)	N			P			X	W	(M)									H										—	10
Gnaphalium candidissimum Lam.	N			P									+		+		+	+					+	+				30	30
G. indicum L. (H)	N		A													H												10	—

APPENDIX I (*Continued*)

Species	Status		Longevity			Life Form						Habitat	Islands round Wilson's Promontory								Wilson's Promontory							South-eastern Victoria					Per Cent. Frequency	
	Native (N)	Introduced (I)	Annuals (A)	Biennials (B)	Perennials (P)	Creeping Plants (C)	Succulents (F)	Sclerophylls (X)	Switch Plants (S)	Xeromorphic Monocotyledons (Z)	Woody Species (W)	Typical Heath Species (M)	Citadel Island	Dannevig Island	McHugh Island	Cliffy Island	Rabbit Island	Granite Island	Benison Island	Doughboy Island	Oberon Bay Dunes	Oberon District Control	SE. Point Lighthouse Control	Three Mile Beach Control	Chinaman's Bay etc. Dunes	Chinaman's Bay etc. Control	Miller's Hut Coast Control	Gabo Island Rookery	Gabo Island Control Area	Mallacoota Bird Roost	Mallacoota Dunes	Mallacoota Control Area	Bird Colonies	Dunes and Control Areas
Compositae (*Continued*)																																		
Gnaphalium involucratum Forst. f. (H)	N		A																	H							+						10	10
G. japonicum Thunb. (H)	N				P															+					H	+							10	20
G. luteo-album L.	N		A													+			+	+				+	+		+	+					40	30
G. purpureum L. (H)	N		A															H										+	+				20	10
Cassinia longifolia R.Br. (H)	N				P						W																				H		—	10
C. spectabilis (Labill.) R.Br.	N				P																								+		+	+	—	30
Helichrysum apiculatum (Labill.) DC. (H)	N				P							M											H										—	10
H. baxteri A. Cunn. ex DC. (H)	N				P							M										H	H										—	20
H. bracteatum (Vent.) Andr. var. *albidum* (H)	N				P									H	H																		20	—
H. dendroideum N. A. Wakefield (H)	N				P			X			W									H				?									10	20
H. gunnii (Hook. f.) Benth. (H)	N				P			X			W										H		H	+		+	+				+		—	60
H. leucopsidium DC. (H)	N				P							M																	H				—	10
H. obcordatum (DC.) Benth. (H)	N				P			X			W																		H				—	10
Calocephalus brownii (Cass.) F. Muell.	N				P			(X)	(S)		W										+	+	+										—	30
Cotula australis (Sieber ex Spreng.) Hook. f.	N				P															+	+	+	+				+						10	40
C. coronopifolia L.	N				P		F									+	+											+	+				30	10
C. vulgaris Levyns var. *australasica* J. H. Willis	N		A																						+								—	10
C. reptans (Benth.) Benth. (H)	N				P	C															H				+		+		H				—	40
Senecio biserratus Belcher (H)	N		A?																	H?		H											10	10
S. elegans L.	N		A				(F)														+	+											—	20
S. hispidulus A. Rich. (H)	N		A?																	+				?				H					20	10
S. lautus Forst. f. ex Willd. (H)	N				P		(F)						H	+	H	+	H	H	H	H	H	+	+	+	+	+	+	+	+				90	80

Senecio linearifolius A. Rich. (H)	N				P																+		H								H		—	30
S. minimus Poir. (H)	N		A?																	H	?						?	+					20	20
Arctotheca calendula (L.) Levyns		I			P																		+						+				—	20
Cymbonotus lawsonianus Gaud.?	N				P																+												—	10
Cirsium vulgàre (Savi) Ten.		I		B														+	+	+			+		+	+		+	+		+		40	50
Carduus tenuiflorus Curt.		I	A	B													+			+													20	—
Hypochaeris glabra L. (H)		I	A	B																H					+								10	10
H. radicata L.		I			P											+			+	+	+		+		+	+	+	+	+				40	60
Leontodon hirtus L. (H)		I		B	P															H			+		H		+	+					20	30
Taraxacum officinale Weber		I			P																		+										—	10
Sonchus asper (L.) Hill		I	A													+				+													20	—
S. megalocarpus (Hook. f.) J. M. Blake	N		A				(F)												+	+	+	+	+		+						+		20	50
S. oleraceus L.		I	A											20		+		+	+	+			+	+	+			+		+			70	30
Total number of species, 360	280	80	66	11	283	95	28	78	6	24	92	84	8	20	18	40	24	17	59	98	63	74	117	69	67	100	72	60	119	10	35	63	166	312
Percentage of natives	78												100	95	100	55	83	75	83	76	89	96	66	94	78	94	86	67	71	50	91	98	78·4	85·9
Percentage of aliens		22											0	5	0	45	17	25	17	24	11	4	34	6	26	6	14	33	29	50	9	2	21·6	14·2
Percentage of annuals and biennials				21									0	15	6	53	25	38	31	33	18	7	27	14	25	10	19	37	18	30	13	4	26·8	15·6
Percentage of perennials					79								100	85	94	47	75	62	69	67	82	93	73	86	75	90	81	63	82	70	87	96	73·2	84·4
Percentage of creeping plants						26							25	25	28	13	30	13	31	19	27	25	26	27	37	24	29	22	34	50	43	38	25·6	30·7
Percentage of succulents							8						50	55	50	35	42	38	19	11	14	7	4	10	20	4	8	20	9	30	16	4	36·0	9·4
Percentage of sclerophylls								22					12	5	11	3	13	13	8	12	26	46	20	34	6	37	24	5	19	0	17	42	8·2	27·9
Percentage of switch plants									2				0	0	0	0	0	0	0	0	2	4	2	4	0	4	3	2	1	0	0	4	0·2	2·4
Percentage of xeromorphic monocotyledons										7			25	10	6	3	13	6	7	5	5	11	10	11	12	7	14	12	8	0	6	8	8·7	9·2
Percentage of woody plants											25		25	15	33	3	21	13	12	15	29	56	24	41	10	40	25	8	21	10	26	50	15·5	32·2
Percentage of typical heath species												23	0	0	0	0	0	0	0	0	8	40	21	33	3	40	18	2	15	0	0	53	0·2	23·2

STUDIES IN THE CUNONIACEAE

I. THE GENERA CERATOPETALUM, GILLBEEA, AISTOPETALUM, AND CALYCOMIS

By R. D. Hoogland*

[*Manuscript received March* 10, 1960]

Summary

This first series of studies in the Cunoniaceae offers revisions of the genera *Ceratopetalum* Sm., *Gillbeea* F. Muell., *Aistopetalum* Schltr., and *Calycomis* D. Don. Full synonymy, bibliography, descriptions, and critical notes are given for the genera and species, and keys to the species are included.

The genus *Ceratopetalum* comprises five species in eastern Australia and New Guinea. *C. tetrapterum* Mattf., described from New Guinea, is reduced in synonymy under *C. succirubrum* C. T. White, previously known only from north-eastern Queensland.

The genus *Gillbeea* comprises two species, one in north-eastern Queensland and one in New Guinea.

The genus *Aistopetalum* comprises two species in New Guinea; one species is widespread in the northern parts of the island, the other is known only from the type collection. *A. tetramerum* Kan. et Hat. is reduced in synonymy under *A. viticoides*.

The genus *Calycomis* is monotypic; its only species, *C. australis* (A. Cunn.) Hoogl. comb. nov. (*Weinmannia australis* A. Cunn.) is found in the Blue Mountains of New South Wales and is currently known as *Acrophyllum verticillatum* or *A. venosum*.

I. Genus CERATOPETALUM Sm.

Ceratopetalum Sm., Specim. Bot. New Holl. **1**: 9, t.3 (1793); Willd., Linn. Sp. Pl., 4th Ed. **2**: 580 (1799); Pers., Syn. Pl. **1**: 471 (1805); Spreng., Linn. Gen. Pl., 9th Ed. **1**: 356 (1830); D. Don in Edinb. New Phil. J. **9**: 94 (1830); DC., Prod. **4**: 12 (1830); G. Don, Gen. Hist. **3**: 202 (1834); Spach, Hist. Nat. Veg. Phan. **5**: 11 (1836); Meisn., Pl. Vasc. Gen. **1**: 138, **2**: 101 (1838); Endl., Gen. Pl. 818 (1839); Benth., Fl. Aust. **2**: 442 (1864); Benth. et Hook.f., Gen. Pl. **1**: 651 (1865); Baill., Hist. Pl. **3**: 377, 449 (1872); Engl. in Engl. et Prantl, Nat. Pfl.fam. **3(2a)**: 100 (1891); Ch. Moore, Handb. Fl. N.S.W. 178 (1893); Engl. in Engl. et Prantl, Nat. Pfl.fam., 2nd Ed. **18a**: 248 (1930); C. T. White in Proc. Roy. Soc. Qd. **47**: 59 (1936), **53**: 216 (1942). *Type species.—C. gummiferum* Sm., only species.

Ceratopetalum § *Meridema* D. Don in Edinb. New Phil. J. **9**: 94 (1830); Endl., Gen. Pl. 818 (1839). *Type species.—C. apetalum* D. Don, new lectotype.

Ceratopetalum § *Euceratopetalum* Endl., Gen. Pl. 818 (1839). *Type species.— C. gummiferum* Sm., only species.

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Large shrubs or small to large trees with decussate trifoliolate or simple (unifoliolate) leaves with connate interpetiolar stipules with collaters. Stipules enclosing terminal bud, resinous, caducous, leaving a transverse scar between opposite leaf-bases. *Leaves* with nerves and venation prominent on both sides, more strongly so below than above, the lateral nerves little stronger than the reticulate (stretched parallel to the lateral nerves) venation. *Inflorescences* terminal or axillary, corymbiform, dichasial in the extreme ramifications. *Flowers* 4–5(–6)-merous; pedicel articulate; sepals valvate, reduplicate; petals membranaceous, 3–5-furcate, or absent; diplostemonous, the episepalous stamens slightly longer than the others; filaments flattened at base, terete towards apex, anthers dorsifixed, cordiform, ± entrorse with longitudinal slit; disk annular, more or less distinctly lobed between the stamens; ovary half-inferior, 2-celled, each cell with 4 epitropous ovules; styles subulate, divergent. *Fruits* surrounded by radiating enlarged woody sepals, indehiscent; carpels slightly woody, each with a single seed.

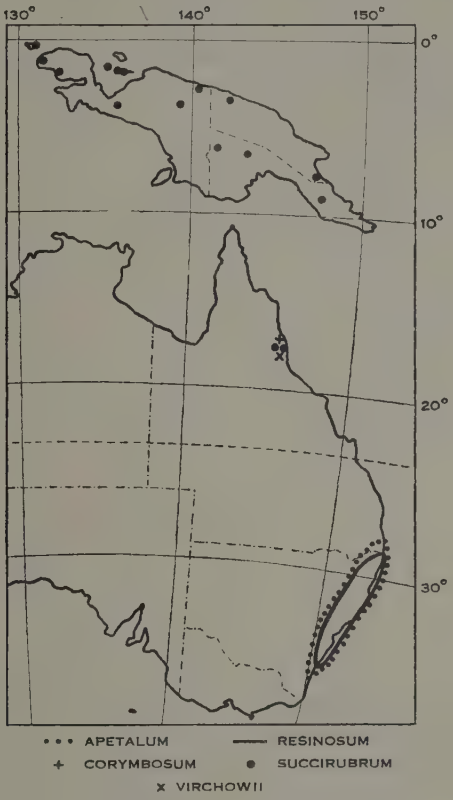

Fig. 1.—Distribution of *Ceratopetalum.*

Distribution.—Eastern Australia (eastern New South Wales and extreme south-eastern Queensland, and a limited area in north-eastern Queensland) and New Guinea (Fig. 1).

The genus is characterized primarily by the fruit being surrounded by the enlarged and lignified sepals. The other cunoniaceous genus in which the sepals are enlarged in fruit, *Aphanopetalum* Endl., differs in its twining habit and by the distinctly less woody and not stellately spreading sepals.

The character to which the genus owes its name, the presence of branched petals (Greek *κερας* = antler), is found only in the type species, all other species being apetalous. A similar type of petals is found in the Cunoniaceae in the genera *Schizomeria* D. Don and *Platylophus* D. Don, which have a different type of fruit.

D. Don (1830) brought his new species *C. apetalum* and *C. montanum* (which are here considered synonymous) together as § *Meridema*, a taxon of which he did not indicate the rank and which he characterized "Foliis simplicibus, floribus apetalis". Endlicher (1839) followed him and named the taxon to which the type species of the genus belongs *Euceratopetalum*, again without indication of rank. The subdivision of the genus in this way is not maintained here, since the three species, described subsequently, combine trifoliolate leaves with apetalous flowers. It is felt that, if the subdivision is maintained, it should be based on the floral character. There is little need for subdivision in this small genus and the difference does not appear to be of great consequence.

KEY TO THE SPECIES OF CERATOPETALUM

1. Leaves simple (unifoliolate), generally about 2–4 times as long as broad. Flowers apetalous. New South Wales and SE. Queensland .... 1. *apetalum*
Leaves trifoliolate 2

2. Leaflets narrow, about 5 times as long as broad. Flowers with 3–5-furcate petals. New South Wales .... 3. *gummiferum*
Leaflets broader, about 2–4 times as long as broad. Flowers apetalous. NE. Queensland and New Guinea 3

3. Flowers 4(–5)-merous, i.e. the large majority of the flowers in one individual 4-merous. NE. Queensland and New Guinea .... 4. *succirubrum*
Flowers (4–)5(–6)-merous, i.e. the large majority of the flowers in one individual 5-merous. NE. Queensland 4

4. Sepals ovate-oblong, *c.* 4·8 by 1·9 mm. Leaflets obovate-oblong, long-decurrent without distinct petiolule .... 2. *corymbosum*
Sepals ovate, *c.* 2·9–3·5 by 1·5–2·5 mm. Leaflets oblong, with cuneate base sharply distinct from the petiolule .... 5. *virchowii*

1. **Ceratopetalum apetalum** D. Don in Edinb. New Phil. J. **9**: 94 (1830); G. Don, Gen. Hist. **3**: 202 (1834); Walp., Rep. Bot. Syst. **5**: 829 (1846); Benth., Fl. Aust. **2**: 442 (1864); Woolls, Contr. Fl. Aust. 92, 176, 204 (1867); F. Muell., Fragm. **6**: 189 (1868), **7**: 150 (1871); F. Muell., Syst. Cens. Aust. Pl. **1**: 48 (1882); Nilson, Timber Trees N.S.W. 43 (1884); F. Muell., Sec. Syst. Cens. Aust. Pl. **1**: 82 (1889); Maiden, Usef. Native Pl. Aust. 403 (1889); Engl. in Engl. et Prantl, Nat. Pfl.fam. **3(2a)**: 100, fig. 57*D*,*E* (1891); Ch. Moore, Handb. Fl. N.S.W. 178 (1893); Maiden, Some N.S.W. Pl. Worth Cultiv. 6 (1896); Maiden, For. Fl. N.S.W. **1**: 127, t.21 (1904); Pamp. in Ann. Bot., Roma **2**: 61 (1905); Maiden, For. Fl. N.S.W. **2**: 196 (1906); Maiden et Betche, Cens. N.S.W. Pl. 88 (1916); Maiden,

For. Handb. **2**: 208, t. (1917); Domin in Bibl. Bot., Stuttgart **89**: 707 (1925); Francis, Aust. Rain-Forest Trees 135 (1929); Engl. in Engl. et Prantl, Nat. Pfl.fam., 2nd Ed. **18a**: 248, fig. 144*D*,*E* (1930); Anderson, Trees N.S.W., 2nd Ed., 221 (1947); Francis, Aust. Rain-Forest Trees, Rev. Ed., 155 (1951). *Type specimen.—Caley* s.n., "*C. monopetalum*", New Holland, in Herb. Lambert, holotype now in BM,* isotypes in A,W.

Ceratopetalum monopetalum Caley ex D. Don in Edinb. New Phil. J. **9**: 94 (1830) in syn. sub *C. apetalum*, invalid name.

Ceratopetalum montanum D. Don in Edinb. New Phil. J. **9**: 94 (1830); G. Don, Gen. Hist. **3**: 202 (1834); Walp., Rep. Bot. Syst. **5**: 829 (1846). *Type specimen.—Caley* s.n., New Holland, in Herb. Lambert, holotype now in BM, isotype in W.

Ceratopetalum apetalum f. *montanum* (D. Don) Pamp. in Ann. Bot., Roma **2**: 61 (1905).

Ceratopetalum apetalum var. *microphyllum* J. F. Bail. et C. T. White in Bot. Bull., Brisbane, No. 18: 6, t.1 (1916); Francis, Aust. Rain-Forest Trees 135 (1929); Engl. in Engl. et Prantl, Nat. Pfl.fam., 2nd Ed. **18a**: 248 (1930); Francis, Aust. Rain-Forest Trees, Rev. Ed., 155 (1951). *Type specimen.—C. T. White* s.n., Springbrook (McPherson Range, SE. Queensland), holotype in BRI, isotypes in A, K.

Ceratopetalum apetalum var. *montanum* (D. Don) Domin in Bibl. Bot., Stuttgart **89**: 707 (1925).

Ceratopetalum apetalum var. *typicum* Domin in Bibl. Bot., Stuttgart **89**: 707 (1925).

Trees, up to 25 m tall, 60 cm dia., often flowering already as a small tree. Twigs when young ± quadrangular, the ridges most pronounced above the leaves; sparsely pubescent, early glabrescent, or glabrous; older ones terete. *Leaves* simple (unifoliolate) (or rarely trifoliolate? cf. note below). Stipules triangular, *c.* 3–5 mm long, 1–2 mm broad, caducous (falling before leaves are fully grown) to subpersistent (falling only little earlier than leaves), glabrous. Petiole *c.* (4–)8–20 (–32) mm long, distinctly channelled, glabrous. Blade (leaflet) oblong to lanceolate, *c.* 15–25-nerved, *c.* (2·5–)6–12(–25) cm long, (8–)25–45(–75) mm broad; apex obtuse to acute, slightly acuminate, base obtuse to acute; margin shallowly dentate to serrate with resinous gland at apex of teeth; glabrous on both sides; sometimes minute, linear-lanceolate or subulate, up to *c.* 2 mm long, stipellae or lateral leaflets present, early caducous, rarely persistent. *Inflorescences* terminal, sometimes with 1 or 2 pairs of reduced leaves in the basal part, or axillary with at most 3 pairs of leaves above them, up to *c.* 12 cm long, 7 cm dia., with up to 8 cm long peduncles; branches ± quadrangular, pubescent, glabrescent; bracts early caducous, consisting of 5 parallel lanceolate to subulate lobes (the 3 central ones sometimes connate) of which central one longest, up to *c.* 2·2 mm long, glabrous. *Flowers* 4–5-

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* All specimens cited in this paper were seen by the author with one exception (the holotype of *Aistopetalum tetramerum*). Abbreviations for the various herbaria are given in accordance with the list published in the "Index Herbariorum", 3rd Ed. (1956).

merous; pedicel articulate up to *c.* 1·2 mm below the flower, pubescent, with bracteoles (like the bracts, up to *c.* 1·4 mm long) below the articulation. Sepals broad-ovate, slightly acuminate at apex, *c.* 3·0–4·3 mm long, 1·8–2·8 mm broad, sparsely pubescent with ± appressed hairs outside, fairly densely puberulous inside. Petals absent. Stamens with *c.* 1·3–2·7 mm long filament; anther with short (0·1 mm) sterile apex, *c.* 0·5–0·6 mm long, 0·5–0·6 mm broad, 0·3–0·4 mm thick. Disk *c.* 0·3–0·8 mm high, 0·2–0·3 mm thick. Ovary *c.* 0·7–1·1 mm high, 1·0–1·2 mm dia., fairly densely puberulous; styles *c.* 1·6–2·5 mm long, ± divergent, glabrous. *Fruit* with sepals enlarged to *c.* 8 by 2 mm; ovary *c.* 4·6 mm long, 3·8 mm dia., the superior part sparsely puberulous.

Distribution.—Eastern side of Dividing Range in New South Wales and extreme south-eastern Queensland (selected localities: NEW SOUTH WALES: Bateman's Bay, Berry, Bundanoon, Robertson, Bulli, Waterfall, Mt. Victoria, Mt. Wilson, Sydney and suburbs, Broken Bay, Gosford, Stroud, Kempsey, Dorrigo, Timbarra, Lismore. QUEENSLAND: Mt. Roberts, Springbrook), common in rainforest. For descriptions of the forest in which the species is dominant, cf. Alan Burges et R. D. Johnston, "The structure of a New South Wales subtropical rain forest", J. Ecol. **41**: 72–83, Figs. 1–8, tt. 3–4, phot. 1–4 (1953), and G. N. Baur, "Nature and distribution of rain-forests in New South Wales", Aust. J. Bot. **5**: 190–233, Figs. 1–3 (1957).

Specimens Studied.—Numerous specimens, mostly unnumbered, e.g. *Bauer* 768, 769; *Bauerlen* 137, 373; *de Beuzeville* 1, 53, 701; *Boorman* s.n.; *R. Brown* 4400; *Caley* s.n.; *Constable* NSW 11303, 11327, 19109; *A. Cunningham* 48; *Gaudichaud* s.n.; *Goy and L. S. Smith* 21; *Hoogland* 6294; *Hügel* s.n.; *Johnson* s.n.; *MacDonald* 221, 224; *McKee* 525; *Meebold* 7589; *Morrison* 5551, 5552; *Govr. Phillip* s.n.; *Rodway* 1030, 2668; *C. T. White* 5090, 6195, 6262, 7525, 8521, 10523, 11389, 11879, s.n.

A number of specimens are aberrant in the distinctly narrower, lanceolate leaflets, *c.* 40–90 by 7–13 mm, and several intermediates between these and the normal form exist. As may be gathered from notes by L. S. Johnson (NSW 41054 and 41055) there is a correlation between habitat and leaf shape: the narrow leaves are found on trees growing on river banks and subject to flooding (rheophytes; cf. C. G. G. J. van Steenis in Proc. Roy. Soc. Qd. **62**: 61–68 (1952)). The type of *C. montanum* D. Don belongs here.

Var. *microphyllum* was based on a specimen from a large tree. A perfect match to this collection is in *C. T. White* 7525 (BRI); this collection consists of vegetative branches from (*a*) young trees and (*b*) large trees felled for timber. The leaves on (*a*) agree with most other collections in leaf size, those on (*b*) with those of the type of var. *microphyllum*. It appears that the leaves on large trees are considerably smaller than those on young trees and that generally only the latter are represented in the herbaria. The description of the species, given above, has largely been based on specimens from such young trees, and the leaf size of large trees falls within the range of *c.* 25–50 by 8–25 mm.

A specimen in MELB (leg. Miss Atkinson) has, in addition to a flowering branch, two loose leaves which are trifoliolate. The following note is with this specimen: "Miss Atkinson reports that *Ceratopetalum apetalum* has leaves sometimes in threes, sometimes simple". The leaves, which are large for the species and may have been collected from a seedling tree or a watersprout, have a stout, *c.* 22 mm long petiole; the central leaflet is *c.* 20 by 7 cm, the lateral ones are *c.* 17 by 5 cm, distinctly asymmetrical; the margins are coarsely dentate. This specimen is the only one in over a hundred I studied with trifoliolate leaves. It is possible, though not likely in view of their size, that the trifoliolate leaves represent *C. resinosum*. However, it will be desirable to study seedlings and watersprouts of the present species in order to find out whether trifoliolate leaves do indeed occur.

The timber of this species was extensively used in the coach-building industry and is still widely used in furniture making. It is known as Coachwood, Lightwood, or Leather Jacket.

2. **Ceratopetalum corymbosum** C. T. White in Proc. Roy. Soc. Qd. **53**: 216 (1942). *Type specimen.—Dr. H. Flecker* (North Queensland Naturalist Club) 7108, Thornton Peak (Cairns district, N. Queensland), holotype in BRI.

Probably trees. Twigs terete to fairly distinctly quadrangular, smooth, glabrous. *Leaves* trifoliolate. Stipules unknown. Petiole *c.* 16–32 mm long, terete, slightly channelled above, glabrous, smooth. Leaflets obovate-oblong, the central one slightly larger than the lateral ones; *c.* 25–50-nerved, *c.* 4–10·5 cm long, 11–28 mm broad; apex obtuse to acute, slightly acuminate, base narrow-cuneate, long decurrent, in the lateral leaflets slightly unequal-sided; margin entire, very distinctly recurved; glabrous and glossy on both sides. *Inflorescences* terminal, with reduced leaves at base, up to *c.* 14 cm long, 12 cm dia.; branches sharply keeled, quadrangular, pubescent, glabrescent; bracts caducous, ovate, up to *c.* 2·7 mm long, 1·8 mm broad, with several marginal glands, caducous. *Flowers* (4–)5(–6)-merous; pedicel articulate up to *c.* 1·5 mm below the flower, sparsely pubescent, with bracteoles (like the bracts, up to *c.* 1·5 mm long) generally just below the articulation. Sepals ovate-oblong, acute to acuminate at apex, *c.* 4·8 mm long, 1·9 mm broad, glabrous or with few hairs towards base outside, inside with *c.* 0·2 mm broad band of very short dense pubescence along margin, glabrous or very sparsely hirsute in central part. Petals absent. Stamens with *c.* 2·4–2·7 mm long filament; anther with very short (<0·05 mm) sterile apex, *c.* 0·5 mm long, 0·5 mm broad, 0·3 mm thick. Disk *c.* 0·4 mm high and thick. Ovary *c.* 0·7 mm high, 0·8 mm dia., glabrous; styles *c.* 3·0 mm long, glabrous. *Fruit* unknown.

Distribution.—North-eastern Queensland, known only from the type collection at 4500 ft altitude.

This little-known species is clearly distinct in its long, narrow sepals and particularly its many-nerved, long-decurrent leaflets.

3. **Ceratopetalum gummiferum** Sm., Specim. Bot. New Holl. 9, t.3 (1793); Willd., Linn. Sp. Pl., 4th Ed. **2**: 580 (1799); Pers., Syn. Pl. **1**: 471 (1805); Spreng., Linn. Syst. Veg., 16th Ed. **2**: 331 (1825); D. Don in Edinb. New Phil. J. **9**: 94 (1830); DC., Prod. **4**: 13 (1830); G. Don, Gen. Hist. **3**: 202 (1834); Spach, Hist. Nat. Veg. Phan. **5**: 11 (1836); Walp., Rep. Bot.

Syst. **5**: 829 (1846); A. Gray, U.S. Expl. Exped. Bot. **1**: 666 (1854); Benth., Fl. Aust. **2**: 442 (1864); F. Muell., Syst. Cens. Aust. Pl. **1**: 48 (1882); Nilson, Timber Trees N.S.W. 43 (1884); F. Muell., Sec. Syst. Cens. Aust. Pl. **1**: 82 (1889); Maiden, Usef. Native Pl. Aust. 237, 404 (1889); Engl. in Engl. et Prantl, Nat. Pfl.fam. **3(2a)**: 100 (1891); Ch. Moore, Handb. Fl. N.S.W. 178 (1893); Maiden, Some N.S.W. Pl. Worth Cultiv. 15 (1896); Maiden, Flow. Pl. Ferns N.S.W. **7**: 71, t.25 (1898); Wildem., Ic. Sel. Hort. Then. **1**: 57, t.14 (1900); Pamp. in Ann. Bot., Roma **2**: 61 (1905); Maiden, For. Fl. N.S.W. **5**: 169, t.186 (1912), 191 (1913); Maiden et Betche, Cens. N.S.W. Pl. 88 (1916); Domin in Bibl. Bot., Stuttgart **89**: 707 (1925); Engl. in Engl. et Prantl, Nat. Pfl.fam., 2nd Ed. **18a**: 248 (1930); Harris, Wild Flow. Aust. 42, 114, t.40 (1938, 2nd Ed. 1948, 3rd Ed. 1952). *Type specimen.*—Probably a specimen in K.

Small tree, up to *c.* 12 m tall, or large shrub. Twigs round, with 2 opposite narrow ridges above the leaves to next internode, glabrous, the older ones terete. *Leaves* trifoliolate. Stipules triangular, 1–1·5 mm long, 1 mm broad, early caducous, glabrous. Petiole *c.* 10–20 mm long, distinctly channelled, glabrous. Leaflets narrowly oblong, the central one generally slightly larger than the lateral ones; *c.* 10–15-nerved, *c.* 30–70 mm long, 6–14 mm broad; apex bluntly acute, often slightly acuminate; base acute, in the lateral leaflets slightly unequal-sided; margin shallowly serrate to dentate with resinous gland at apex of teeth; glabrous on both sides; dark green above, paler green, often slightly glaucous, below. *Inflorescences* terminal, usually with 1 or 2 pairs of reduced leaves in basal part, up to *c.* 10 cm long, 5 cm dia.; branches more or less quadrangular, glabrous; bracts caducous, small, up to 1·5 mm long, consisting of 3 or 5 parallel, appressed, fleshy, lanceolate to subulate lobes embedded in resin. *Flowers* (4–)5(–6)-merous; pedicel articulate up to *c.* 2 mm below the flower, glabrous, with bracteoles (like the bracts, up to *c.* 1 mm long) below the articulation. Sepals broad-ovate, blunt at apex, *c.* 2·9–3·2 mm long, 1·4–1·8 mm broad; glabrous outside; fairly long thin-strigose in central-basal part, with short erect hairs in lateral-apical part inside. Petals thin, 3-furcate, *c.* 2·8–3·0 mm long, the basal trunk *c.* 0·6–0·9 mm long, 0·4–0·5 mm broad, the lateral forks often bifurcate at *c.* 0·4–0·6 mm from their base, the forks *c.* 0·1–0·2 mm broad, glabrous. Stamens with *c.* 2·7–3·0 mm long filament; anther with *c.* 0·4 mm long sterile apex, *c.* 0·9 mm long, 0·5 mm broad, 0·3 mm thick. Disk *c.* 0·9 mm high, 0·2 mm thick. Ovary *c.* 0·7 mm high, 0·8 mm dia., glabrous; styles *c.* 1·7 mm long, connivent for *c.* 1·2 mm, the upper part curving outward to ± horizontal position, glabrous. *Fruit* with sepals, deep red, rarely white, enlarged to *c.* 10 by 3·5 mm; petals persistent, slightly woody, *c.* 5 mm long; ovary *c.* 3 mm long, 2·5 mm dia., with *c.* 3 mm long styles.

Distribution.—Eastern side of Dividing Range in New South Wales (selected localities: Jervis Bay, Nowra, Katoomba, Springwood, Sydney and suburbs, Gosford, Stroud, Camden Haven, Wooli, Copmanhurst, Whian Whian State Forest), common in rain-forest and sclerophyll forest.

Specimens Studied.—Numerous specimens, mostly unnumbered, e.g. *Backhouse* 325; *Baker* s.n.; *Bauer* s.n.; *Boorman* s.n.; *R. Brown* 4399; *Caley* s.n.; *Camfield* s.n.; *Constable* NSW 5296, 11314, 11315, 11320; *A. Cunningham* 182, s.n.; *R. Cunningham* s.n.; *Delessert* 24; *Gaudichaud* 28; *Helms* 80, 245; *Hollway* 12; *Hoogland* 6295; *Hügel* s.n.; *Johnson* 270, s.n.; *Leickhardt* s.n.; *MacArthur* 183; *Meebold* 3050, 3141, 7599, 8062; *Govr. Phillip* s.n.; *Raoul* s.n.; *Rodway* 110, 979, 3019, 14418, 15347, s.n.; *Salasov* 609; *Sieber* 260, 540; *Simson* 1627; *Verreaux* 240, 246, 546; *Vieillard* s.n.; *C. T. White* 10341, 12757; *Woolls* s.n.

In *L. S. Johnson* s.n. (NSW 41087) the leaflets are up to 14 cm long, 4 cm wide; this specimen represents a shade shoot of the species.

Ceratopetalum gummiferum is commonly known in New South Wales as Christmas Bush. The species is generally in fruit in the second half of December, and branches with the bright red fruiting calyces and deep green leaves are much valued as a Christmas decoration.

4. **Ceratopetalum succirubrum** C. T. White in Proc. Roy. Soc. Qd. **47**: 59 (1936); Francis, Aust. Rain-Forest Trees, Rev. Ed., 413, figs. 253, 254 (1951). *Type specimen.—J. L. Tardent* s.n., Gadgarra (Atherton Tableland, NE. Queensland), holotype in BRI, isotypes in A, B, K, NY.

Ceratopetalum tetrapterum Mattf. in J. Arnold Arbor. **20**: 432 (1939); Kan. et Hat. in Bot. Mag., Tokyo **56**: 108 (1942); Perry in J. Arnold Arbor. **30**: 150 (1949). *Type specimen.—Brass* 7405, Oroville Camp (Fly R., SE. New Guinea), holotype in B, isotypes in BM, BO, BRI, L.

Geissois sp. Swain, Timb. For. Prod. Qd. 190 (1928).

Ceratopetalum virchowii auct. non F. Muell.; C. T. White, Aust. For. J. **12**: 19 (1929).

Trees, up to *c.* 35 m tall with up to 27 m bole, up to 60 cm dia., with small buttresses, with red-brown or dark brown bark exuding a red sap. Twigs terete or slightly flattened in the plane of the leaves under the nodes, smooth, glabrous. *Leaves* trifoliolate, occasionally bifoliolate, sometimes the opposite pair slightly unequal-sized. Stipules triangular, *c.* 3 mm long, 2·3 mm broad, caducous, glabrous. Petiole *c.* (8–)12–35(–50) mm long, flattened to shallowly channelled in the lower half to two-thirds, gradually to shallowly to deeply channelled in the upper part, glabrous or sparsely strigose, glabrescent, in the lower third part only, smooth. Leaflets distinctly petiolulate; petiolule *c.* (1–)3–15 mm long, convex to distinctly channelled above, glabrous, that of central leaflet *c.* $1\frac{1}{4}$–$1\frac{1}{2}$ times as long as those of lateral ones; blades obovate-oblong or oblong to obovate-lanceolate or lanceolate, the central one slightly (±10 per cent.) larger than the lateral ones; *c.* (3·5–)5·5–12(–14) cm long, (10–)15–50(–55) mm broad, *c.* 25–35-nerved; apex acute to obtuse or rounded; base narrow-cuneate, decurrent, in the lateral leaflets slightly to distinctly unequal-sided; margin faintly serrate to entire, sometimes slightly recurved; glabrous and faintly glossy on both sides. *Inflorescences* terminal, sometimes with 1 or 2 pairs of reduced leaves in basal part, up to *c.* 20 cm long, 12 cm dia. (20 cm dia. in fruit), sometimes at lowest node 1 or 2 collateral branches with each lateral branch; branches ± quadrangular, with dense persistent short pubescence; bracts caducous, ovate-lanceolate, up to *c.* 3·5 mm long, 1·0 mm broad, with small linear glandular lobes on either side about two-thirds up and at apex, sparsely hirsute below, glabrous above, ciliate at margin. *Flowers* 4(–5)-merous; pedicel articulate up to *c.* 2·0 mm below the flower, fairly densely short-hirsute to strigose-hirsute with bracteoles (like bracts, up to *c.* 1·5 mm long) generally just below articulation. Sepals ovate, acute at apex, *c.* 3·2 mm long, 1·8–2·5 mm broad; rather sparsely thin-strigose outside; with *c.* 0·2–0·3 mm broad band of dense very short pubescence along margin, fairly densely hirsute with longer hairs in central part inside.

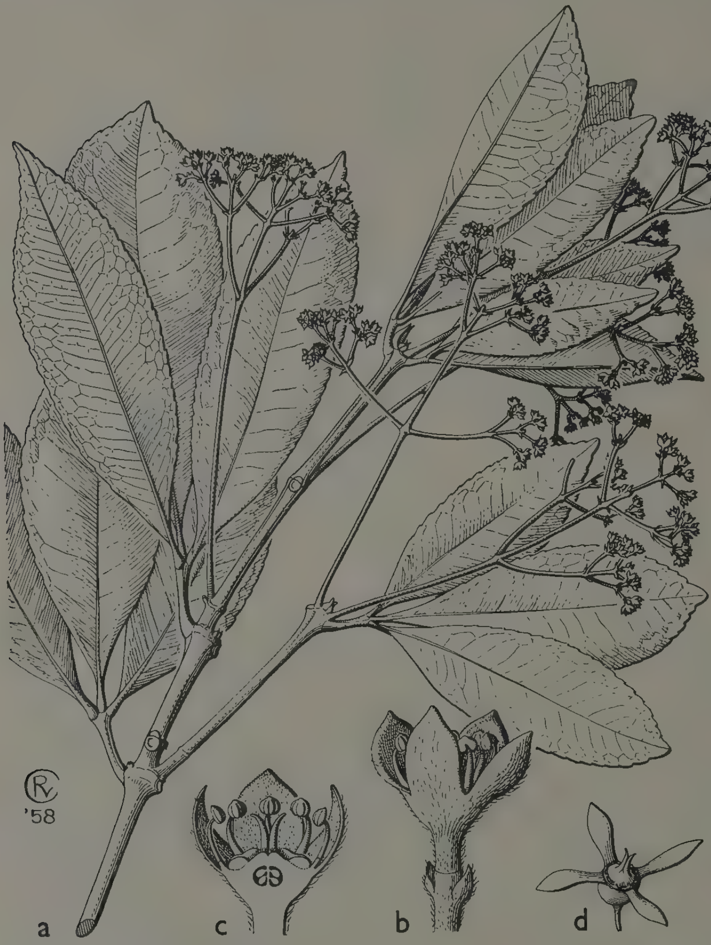

Fig. 2.—*Ceratopetalum succirubrum* C. T. White. *a*, Flowering branch, × ½; *b*, open flower, × 5; *c*, longitudinal section of flower, × 5; *d*, fruit, natural size. (*a*, After *Van Royen* 3198; *b*, *c*, after BW 1163; *d*, after *Brass* 7405.)

Petals absent. Stamens with *c.* 0·9–1·5 mm long filament; anther with up to *c.* 0·2 mm long sterile apex, *c.* 0·3–0·5 mm long and broad, 0·15–0·2 mm thick. Disk *c.* 0·4–0·5 mm high, 0·3 mm thick. Ovary 0·7–0·8 mm high, 0·7–0·9 mm dia., fairly densely hirsute; styles *c.* 0·8–1·2 mm long, slightly curved outward at apex, glabrous or sparsely hirsute at base only. *Fruit* with sepals enlarged to 12 by 3·5 mm; ovary *c.* 5 mm long, 3 mm dia., with *c.* 2 mm long styles (Fig. 2).

Distribution.—Atherton Tableland in north-eastern Queensland (Gadgarra, Danbulla); and widespread in western (Waigheo, Sorong, Ramoi, Beriat), north-western (Miosnom, Ansus, Seroei on Schouten Is.; Boemi; Cyclops Mts. near Hollandia; Bernhard Camp, Idenburgh R.), south-western (Upper Digoel), north-eastern (Torricelli Mts., Wareo), and south-eastern (Oroville Camp, Fly R.; Lake Kutubu; Boridi) New Guinea.

Specimens Studied.—QUEENSLAND: *Dreghorn* s.n.; *Fraser* s.n.; *Tardent* s.n.; *C. T. White* 1571. NEW GUINEA: *Beccari* P. P. s.n.; *Brass* 7405; *Brass and Versteegh* 12516, 13162, 13183; *Carr* 13369; *Cheeseman* 1155, 1156; *Clemens* 1618; *Gray* NGF 8138; *Kalkman* BW 6261; *Kanehira and Hatusima* 12801; *Koster* BW 1163; NIFS bb 14524, 30300, 30301, 30324, 30328, 30374, 30382, 30416; *Pleyte* 745; *Van Royen* 3198; *Schram* BW 1989; *White* NGF 10351.

The species owes its specific epithet and one of its Australian names, "Blood-in-the-bark", to the red exudate of the bark, which has been recorded from New Guinea as well as from Queensland. The name "Satin Sycamore" has been adopted by the Queensland Forest Service as the official name for the timber. Only two names are recorded from New Guinea: "Namajacob" (Digoel) and "Berai" (Tehid language, Beriat).

There is no justification for maintaining *C. tetrapterum* as a distinct species. The specimens from Australia and New Guinea respectively show the same range of variability.

The timber is used in northern Queensland for house-building and for furniture (Swain 1928). No information is available from New Guinea about its uses.

C. T. White (1936) gives a list of field characters in which the species differs from *C. virchowii*. *C. succirubrum* favours richer soils and heavy forest, the crown is light, the flowering time is different, the wood is less heavy, and the exudate is more abundant.

5. **Ceratopetalum virchowii** F. Muell. in Vict. Nat. **7**: 181 (1891); F. M. Bail. in Bull. Qd. Dep. Agric. No. 7: 10 (1891); F. M. Bail., Qd. Fl. **2**: 539 (1900); F. M. Bail., Compr. Cat. Qd. Pl. 169, fig. 139 (1913); Engl. in Engl. et Prantl, Nat. Pfl.fam., 2nd Ed. **18a**: 248 (1930); Francis, Aust. Rain-Forest Trees, Rev. Ed., 418, fig. 255 (1951). *Type specimen.*—*S. Johnson* s.n., Mt. Bartle Frere (NE. Queensland), 1891, holotype in MELB.

Trees. Twigs terete, at most with faint opposite ridges above the leaves to the next internode, glabrous. *Leaves* trifoliolate, occasionally bifoliolate. Stipules ovate-oblong, *c.* 5 mm long, 1–2 mm broad, caducous, glabrous. Petiole *c.* (10–)20–30(–50) mm long, channelled above from indistinctly to shallowly in lower half to two-thirds to deeply in upper part, glabrous. Leaflets distinctly petiolulate; petiolule *c.* 5–22 mm long, deeply channelled above, glabrous, that of central leaflet *c.* 1½ times as long as those of lateral ones; blades oblong, the central one slightly (*c.* 10 per cent.) larger than the lateral ones; *c.* (4–)6–12(–17) cm long, (10–)16–32(–55) mm broad, *c.* (20–)25–30-nerved; apex distinctly acuminate; base cuneate, in the lateral leaflets distinctly unequal-sided; margin repandous or faintly serrate, often slightly recurved; glabrous and faintly glossy on both sides. *Inflorescences* terminal, leafless, up to *c.* 7 cm long, 6 cm dia. (8 cm long, 10 cm dia. in fruit); branches ± quadrangular, short-pubescent, the pubescence persistent; bracts caducous, ovate-lanceolate, up to *c.* 3·5 mm long, 1·0 mm broad, usually with small glandular lobes at base and one pair 0·3–0·8 mm above base, glabrous. *Flowers* (4–)5(–6)-merous; pedicel articulate up to *c.* 1·0 mm below flower, sparsely strigose; bracteoles (like bracts, up to *c.* 2·0 mm long) generally just above articulation. Sepals ovate, acute, distinctly acuminate at apex, *c.* 2·9–3·5 mm long, 1·5–2·5 mm broad; sparsely strigose outside; with *c.* 0·3–0·5 mm broad band of dense very short pubescence along margin, sparsely hirsute with longer hairs in central part inside. Petals absent. Stamens with *c.* 1·6–1·8 mm long filament; anther with *c.* 0·05 mm long sterile apex, *c.* 0·5 mm long, 0·4 mm broad, 0·3 mm thick. Disk *c.* 0·7 mm high, 0·7 mm thick. Ovary *c.* 1·0 mm high, 0·7 mm dia., sparsely hirsute at base, glabrous in upper part; styles *c.* 2·4 mm long, curved in upper part, glabrous. *Fruit* with sepals enlarged to *c.* 12 by 5 mm; ovary *c.* 4·2 mm long and dia. with *c.* 2·5 mm long styles.

Distribution.—North-eastern Queensland: Atherton Tableland (Gadgarra, Yungaburra), Mt. Bellenden Ker, Mt. Bartle Frere, in rain-forest at *c.* 3000 ft altitude.

Specimens Studied.—*Dreghorn* s.n.; *Stephen Johnson* s.n.; *L. S. Smith* 4230.

EXCLUDED SPECIES

Ceratopetalum ovatum Caley ex D. Don in Edinb. New Phil. J. **9**: 95 (1830) in syn. sub *Schizomeria ovata* D. Don, invalid name = *Schizomeria ovata* D. Don.

II. GENUS GILLBEEA F. Muell.

Gillbeea F. Muell., Fragm. **5**: 17 (1865); Baill., Hist. Pl. **3**: 379, 451 (1872); F. M. Bail., Synops. Qd. Fl. 152 (1883); Engl. in Engl. et Prantl, Nat. Pfl.fam. **3(2a)**: 97, fig. 56*A–C* (1891); F. M. Bail., Qd. Fl. **2**: 538 (1900); Schltr. in Bot. Jb. **52**: 144 (1914); Engl. in Engl. et Prantl, Nat. Pfl.fam., 2nd Ed. **18a**: 241 (1930). *Type species.*—*G. adenopetala* F. Muell., only species.

Medium-sized to large trees with decussate impari-pinnate, 1–4(–6)-jugate leaves with terminal leaflet equal-sized to or slightly larger than lateral ones of upper pair, other lateral ones gradually smaller towards base, opposite; with free interpetiolar stipules, the stipular scars of opposite leaves remote or touching, not confluent. *Inflorescences* terminal or axillary, paniculate, many-flowered; only lower branches decussate, otherwise ± spirally arranged. *Flowers* 5(–6)-merous; sepals valvate; petals membranaceous, cuneiform with retuse apex, with small glands at lateral apices, shorter than sepals; stamens 10 (or 12), episepalous ones distinctly longer than epipetalous ones; filament terete, slightly flattened at base, anther cordiform; disk annular, more or less distinctly 10 (or 12)-lobed; ovary superior, 3-celled, each cell with a free style and with 2 or 4 (occasionally 3) ovules. *Fruits* 3-winged, each wing formed by laterally expanded carpel; indehiscent; each carpel with a single seed.

Distribution.—North-eastern Queensland and north-eastern New Guinea (Fig. 3).

The genus is characterized by the shape and structure of the petals, in particular the presence of small glands at the lateral apices, and the structure of the fruit with its firm though relatively thin wings. It was named in honour of Dr. W. Gillbee, surgeon and active promoter of the exploration of tropical Australia.

The two species recognized are obviously closely related. The key enumerates the distinguishing characters in the sequence of their importance. The number of ovules indeed appears to be the most reliably constant character. The petals appear to be always ciliate in the Australian collections, though the number of cilia is variable and actually only a few may be present. Flower size, though quite obvious when directly comparing herbarium specimens of the two species, cannot be expected to be a fully reliable character when the variations come so close together; it is mainly visible in the shape and size of the sepals. A hirsute fruit is found in some of the Australian collections, but even then the young ovary is glabrous.

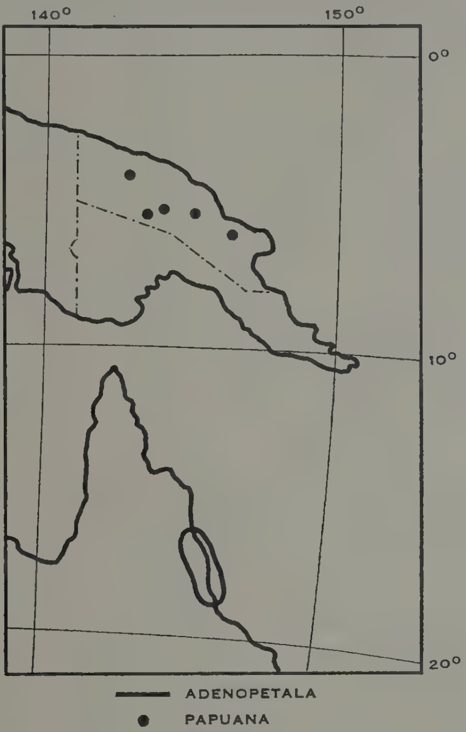

Fig. 3.—Distribution of *Gillbeea*.

Key to the Species of Gillbeea

1. Each carpel with 4 (occasionally 3) ovules. Petals ciliate along lateral margins (at least in lower part). Flowers relatively large, sepals *c.* 4·0–4·6 mm long, *c.* 2–2½ times as long as broad. Ovary glabrous in flower, sometimes developing a stellate-hirsute indumentum in fruit. Inflorescence terminal. NE. Queensland .... **1.** *adenopetala*

Each carpel with 2 ovules. Petals not ciliate. Flowers rather small, sepals up to 3·5, rarely 4·0 mm long, *c.* 1½–2 times as long as broad. Ovary hirsute. Inflorescence axillary. New Guinea .... **2.** *papuana*

1. **Gillbeea adenopetala** F. Muell., Fragm. **5**: 17 (1865), **6**: 180 (1866), 188 (1868); F. Muell., Syst. Cens. Aust. Pl. **1**: 48 (1882); F. M. Bail., Synops. Qd. Fl. 152 (1883); F. Muell., Sec. Syst. Cens. Aust. Pl. **1**: 83 (1889); Engl. in Engl. et Prantl, Nat. Pfl.fam. **3(2a)**: 98, fig. 56*A–C* (1891); F. M. Bail., Qd. Fl. **2**: 539 (1900); Pamp. in Ann. Bot., Roma **2**: 52 (1905); F. M. Bail., Compr. Cat. Qd. Pl. 169 (1913); Domin in Bibl. Bot., Stuttgart **89**: 707 (1925); Engl. in Engl. et Prantl, Nat. Pfl.fam., 2nd Ed. **18a**: 241, fig. 142*A–C* (1930); C. T. White in Contr. Arnold Arbor. No. 4: 40 (1933). *Type specimen*.—(*Dallachy* s.n.), Rockingham Bay (NE. Queensland) in MEL; one sheet with flowering specimen in the Melbourne herbarium selected as lectotype from numerous specimens, often incompletely labelled and certainly partly collected subsequent to the original publication.

Trees, up to 20 m tall; bark dark grey, fairly smooth with very small pustules (fide *Kajewski* 1429). Twigs terete, densely hirsute, glabrescent, the older ones smooth; small stipular scars of opposite leaf-bases not reaching each other (at least 1 mm apart). *Leaves* 1–4, generally 2–3-jugate, *c*. (10–)15–30 cm long. Stipules early caducous, falcate-elliptic, strongly unequal-sided (side towards petiole narrowest), *c*. 6–10 mm long, 3–4 mm broad; with distinct midrib; obtuse to acute at apex, acute at base, densely strigose-hirsute below, sparsely so above. Petiole *c*. 3–12 cm long, terete, channelled above, strigose-hirsute, glabrescent; internodes of rachis *c*. 2·5–6(–9) cm long. Leaflets elliptic or obovate, *c*. 7–14-nerved, *c*. (3–)6·5–15(–21) cm long, (2–)3–7(–10) cm broad; apex obtuse to rounded or retuse, generally with a small broad acumen, base rounded to obtuse (to acute), slightly decurrent; margin dentate with teeth small but very distinct, about 2–3 times as many as lateral nerves; fairly sparsely hirsute, glabrescent, above, rather more densely so and often not quite glabrescent below; petiolule of terminal leaflets *c*. 4–20, of lateral ones *c*. 2–12 mm long. *Inflorescences* terminal, lower branches in axil of reduced leaves; up to *c*. 40 cm long, 20 cm dia.; branches terete or slightly flattened, densely short stellate-hirsute, glabrescent in lower part of inflorescence; bracts small, ovate, up to *c*. 1·5 mm long, 1·0 mm broad, densely hirsute, some of the hairs along margin thicker and with minute apical gland. *Flowers* with *c*. 0·5–2 mm long pedicel with small bracteole, 5(–6)-merous. Sepals triangular-ovate to ovate-oblong, *c*. 4·0–4·6 mm long, 1·8–2·0 mm broad with up to 0·3 mm long hairs in stellate fascicles on base of very short farinose pubescence outside, sparsely hirsute in central part, densely farinose-pubescent along margin inside. Petals *c*. 2·0–2·2 mm long, 1·0–1·4 mm broad, ciliate at lateral margins. Stamens with *c*. 2·0–2·6 resp. 1·7–2·2 mm long, at apex terete (*c*. 0·05 mm dia.), towards base thicker and broadened filament and oval, *c*. 0·4 mm long and broad, 0·2 mm thick anther. Disk *c*. 0·4 mm high and broad, smooth and glabrous. Ovary *c*. 0·8–1·3 mm high, 1·0–1·4 mm dia., glabrous, each cell with (3 or) 4 ovules; styles terete, *c*. 0·3 mm long, glabrous. *Fruits* with obovate, *c*. 18 mm long, 6 mm broad wings coherent along 14 mm long central axis, rounded at apex, with entire margin, glabrous or with numerous stellate groups of short hairs; wings with distinctly prominent venation. Seed oblong, *c*. 6·8 mm long, 0·8–1·0 mm dia., strongly resinous.

Distribution.—High-rainfall area of north-eastern Queensland (Daintree R., Kuranda, Malanda, Boonjie, Ravenshoe, Russell R., Johnstone R., Innisfail, Clump Mt., Tully R., Mission Beach area, Dalrymple Gap) in rain-forest from sea-level to *c.* 750 m altitude; flowering season October to December.

Specimens Studied.—Bancroft s.n.; *Bick* s.n.; *Clemens* s.n.; *Dallachy* s.n.; *Doggrell* s.n.; *Feldt* s.n.; *Fitzalan* s.n.; *Flecker* NQNC 3827, 5301, 6478; *Hayes* s.n.; *Hunt* s.n.; *Johnson* s.n.; *Kajewski* 1429; *Ladbrook* s.n.; *Manuell* 18; *Sayer* 215, 269; *Smith and Webb* 3364, 4793, 4830, 4830A; *Volck* s.n.

Kajewski 1429 has flowers and fruits in various stages of development and shows that hairs develop on the ovary during and after flowering. The flower buds analysed all have a completely glabrous ovary; the study of open flowers reveals that hairs begin to appear in the mature flower near the apex of the ovary and that very soon the whole ovary is covered with hairs. The indumentum on an ovary approximating the sepals in size (i.e. *c.* 3 mm long, *c.* 2–3 times as long as in the just open flower) is still fairly open; it appears to reach its maximum density when the ovary is *c.* 7 mm long. Mature ovaries are less densely hairy again, which indicates that during further growth (to *c.* 18 mm) no or few additional hairs have been formed. In most other collections the ovary appears to remain glabrous.

2. **Gillbeea papuana** Schltr. in Bot. Jb. **52**: 146, fig. 3 (1914); Engl. in Engl. et Prantl, Nat. Pfl.fam., 2nd Ed. **18a**: 241, fig. 141 (1930); Perry in J. Arnold Arbor. **30**: 139 (1949). *Type specimen.—Schlechter* 17191, Kani Mts. (NE. New Guinea), holotype in B, isotype in P.

Gillbeea ledermannii Engl. in Engl. et Prantl, Nat. Pfl.fam., 2nd Ed. **18a**: 241 (1930). *Type specimen.—Ledermann* 10694, Hauptlager Malu, Sepik R. (NE. New Guinea), new lectotype in B.

Tall trees, up to *c.* 30 m high, 35 cm dia., with up to *c.* 12 m tall straight bole; dark brown, fairly smooth. Twigs subterete, compressed under the leaf pairs, densely short strigose-hirsute, glabrescent, the older ones fairly rough; stipular scars of opposite leaf-bases touching but not confluent. *Leaves* (2–)3–4(–6)-jugate, *c.* 10–20 cm long. Stipules often long persistent, obovate or about orbicular, strongly unequal-sided (side towards petiole much narrower than other side), *c.* 10–12 mm long, 7–9 mm broad; with distinct midrib and nerves; obtuse to rounded at apex, obtuse or rounded to cordate at base; fairly densely short strigose-hirsute, glabrescent, above and below. Petiole *c.* 25–45 mm long, terete, channelled above, fairly densely short strigose-hirsute, glabrescent; internodes of the rachis *c.* 12–22 mm long. Leaflets ovate or elliptic, *c.* (8–)10–15-nerved, 5–9·5 cm long, 20–37 mm broad; apex acute to obtuse, slightly acuminate, base obtuse, slightly decurrent, slightly unequal-sided in lateral leaflets; margin entire, slightly recurved; glabrous except for some short strigose hairs along midrib above, sparsely strigose-hirsute, glabrescent on intervenium, more densely so with at least part of indumentum persistent on midrib and basal part of nerves below; petiolule *c.* 2–5 mm long. *Inflorescences* axillary, usually 2 serially placed, the upper one about twice as strong as the lower one, up to 25 cm long, 15 cm dia.; branches subterete, densely

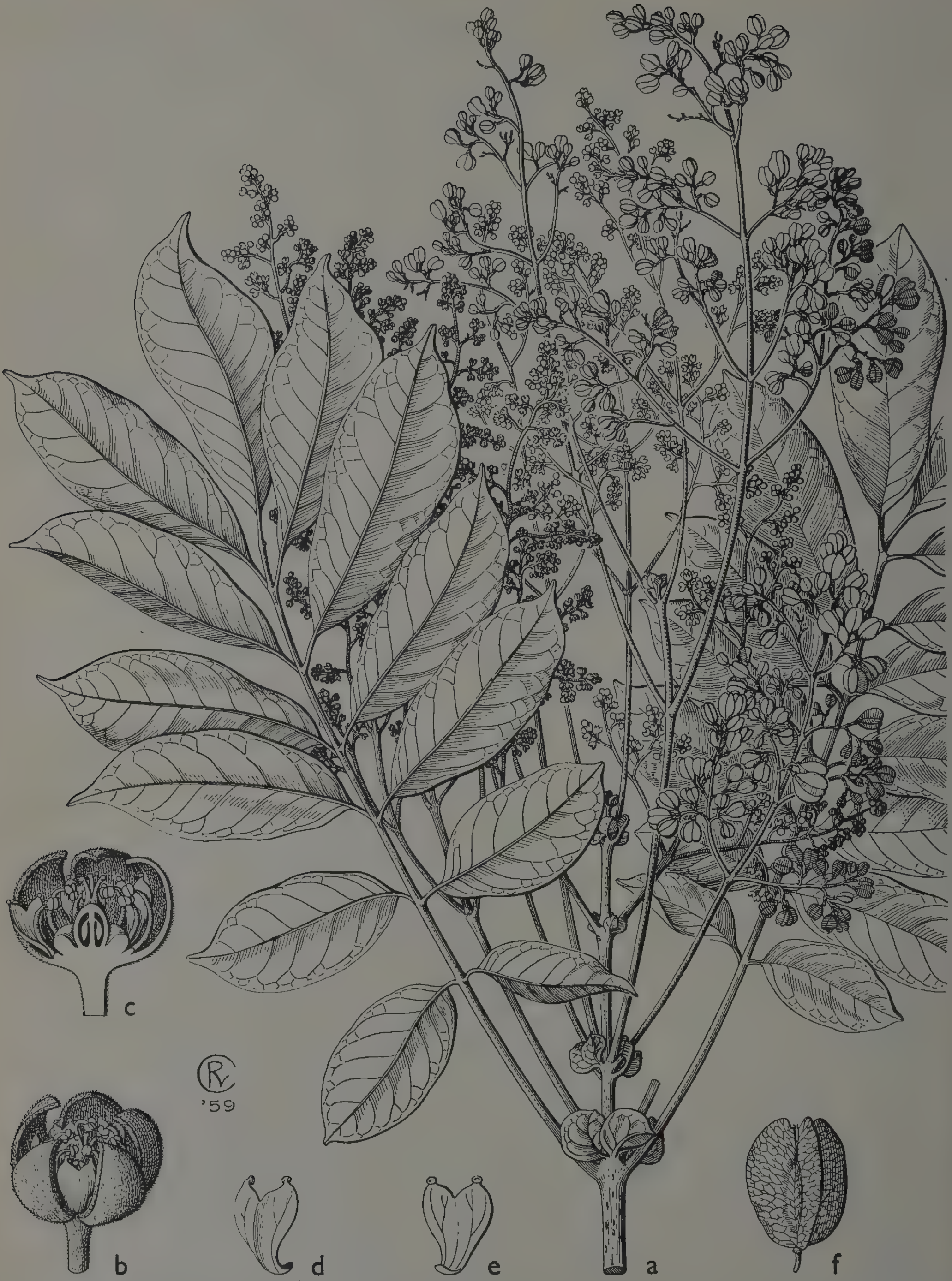

Fig. 4.—*Gillbeea papuana* Schltr. *a*, Branch with flowers and immature fruit, ×½; *b*, open flower, ×5; *c*, longitudinal section of flower, ×5; *d*, *e*, petal, ×8; *f*, fruit, natural size. (*a*, After *Ledermann* 10694; *b–e*, after *Hoogland and Pullen* 5873; *f*, after *Ledermann* 6772.)

short-hirsute in upper, sparsely so in basal part of inflorescence; bracts small, ovate or rhomboid, up to *c.* 3·2 mm long, 1·8 mm broad, densely short-hirsute, with some minute glands at margin, early caducous. *Flowers* with *c.* 0·8–3·0 mm long, distinctly articulate pedicel, 5-merous. Sepals ovate or broad-ovate *c.* 3·0–4·0 mm long, 1·2–3·3 mm broad, densely short stellate-hirsute outside, sparsely hirsute in central part, densely short pubescent along margin inside. Petals *c.* 1·7–2·6 mm long, 0·6–1·7 mm broad, not ciliate at margin. Stamens with *c.* 1·3–2·4 resp. 1·0–2·0 mm long, at apex terete (0·05 mm dia.), towards base thicker and flattened filament and oval, *c.* 0·3–0·4 mm long and broad, 0·2–0·3 mm thick anther. Disk up to *c.* 0·6 mm high, 0·8 mm thick, smooth and glabrous. Ovary *c.* 0·8–1·1 mm high, 0·9–1·0 mm dia., short hirsute, each cell with 2 ovules; styles terete, *c.* 0·5 mm long, glabrous. *Fruits* with obovate, *c.* 16–18 mm long, 6 mm broad wings coherent along 14–16 mm long central axis, rounded at apex, with entire, slightly undulate margin, with numerous stellate groups of short hairs; wings with distinctly prominent reticulate venation, generally at right angles to central axis. Seed oblong, *c.* 5 mm long, 0·8 mm dia., with very short ± glandular hairs (Fig. 4).

Distribution.—Known from some localities in north-eastern New Guinea (Mt. Hagen, Wahgi-Jimmi Divide, Malu, Kani Mts., Yoangen), in primary forest from 50 to 2300 m altitude.

Specimens Studied.—*J. and M. S. Clemens* 3430, 3769; *Hoogland and Pullen* 5873; *Ledermann* 6772, 7420, 7884, 10351, 10694; *Robbins* 601; *Schlechter* 17191, 17283.

Of the specimens collected by Ledermann and annotated by Engler, still present in the Berlin herbarium, I have selected the flowering specimen, No. 10694, as the lectotype for *G. ledermannii*. Engler's description is extremely short, but there can be no doubt that his publication of the binomial is valid. The differences with *G. papuana*, indicated by Engler, do not justify the distinction of a separate species. His main distinguishing character is the shape of the petals, these being "länglich" in *G. papuana*, "breit keilförmig" in *G. ledermannii*. The shape of the petals apart from being variable generally, even within one flower, depends to a considerable extent on the stage of the flower. Those of the type of *G. papuana* are generally less narrow than the one illustrated by Schlechter. Those of *Ledermann* 10694 are indeed exceptionally broad, but most later collections of the species are intermediate between these two extremes.

Schlechter's illustration (1914; reproduced by Engler, 1930) is wrong in showing the stipules as being connate; the opposite stipules are free and narrower than figured.

III. GENUS AISTOPETALUM Schltr.

Aistopetalum Schltr. in Bot. Jb. **52**: 142 (1914); Engl. in Engl. et Prantl, Nat. Pfl.fam., 2nd Ed. **18a**: 239, fig. 138 (1930); Perry in J. Arnold Arbor. **30**: 158 (1949). *Type species.*—*A. viticoides* Schltr., new lectotype.

Tall trees with decussate, impari-pinnate, 1–2-jugate, occasionally unifoliolate leaves with terminal leaflet slightly larger than lateral ones, upper lateral ones slightly larger than lower ones; with early caducous connate interpetiolar stipules with collaters; stipular scar a continuous arc between opposite leaf-bases. *Inflorescences* axillary, paniculate, many-flowered. *Flowers* 4–6-merous, apetalous; sepals valvate; stamens 8, 10, or 12, the episepalous ones longest; filament terete, anther cordiform; disk annular, more or less distinctly 4–6-angular; ovary superior, with 4–6 closely connate cells, each with 1 pendulous ovule. *Fruit* drupaceous with dry-leathery exocarp and woody endocarp, with 4–6 seeds.

Distribution.—New Guinea (Fig. 5).

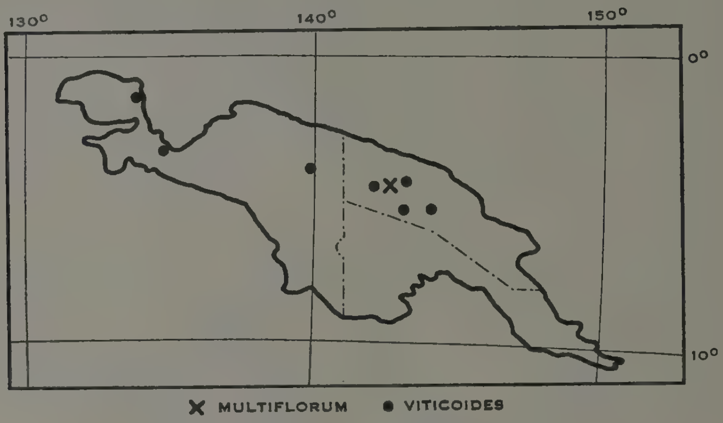

Fig. 5.—Distribution of *Aistopetalum.*

The woody, indehiscent fruit characterizes the genus. It differs from *Schizomeria*, which has a similar fruit, by the number of carpels (2 in *Schizomeria*) and the number of ovules per cell (4 in *Schizomeria*), and also by the compound leaves (simple or unifoliolate in *Schizomeria*) and the absence of petals. The latter two characters, however, may vary within one genus in the Cunoniaceae (e.g. *Ceratopetalum*).

The generic name is derived from the absence of petals (Greek *α* = not, *ιστο* = is present).

Key to the Species of Aistopetalum

1. Leaflets *c.* 18–20 nerved; inflorescences many-flowered (*c.* 250 or more flowers); disk very densely short-hirsute .... 1. *multiflorum*
Leaflets *c.* (10–)12–15-nerved; inflorescences relatively few-flowered (up to *c.* 50 flowers); disk glabrous .... 2. *viticoides*

1. **Aistopetalum multiflorum** Schltr. in Bot. Jb. **52**: 143, fig. 2*G–L* (1914); Engl. in Engl. et Prantl, Nat. Pfl.fam., 2nd Ed. **18a**: 239, fig. 138*G–L* (1930). *Type specimen.—Ledermann* 8531, Hunstein Range, Quellenlager (NE. New Guinea), holotype in B.

Tall trees, up to *c.* 30 m high; bark grey-brown. Twigs rather distinctly flattened under the leaf pairs, the older ones terete; very sparsely minutely strigose, early glabrescent. *Leaves* trifoliolate. Stipules ovate-oblong, up to *c.* 3 mm long, 1·5 mm broad, densely minutely strigose below. Petiole *c.* 25–35 mm long, terete, slightly channelled above, glabrous or very sparsely minutely strigose. Leaflets oblong or obovate-oblong; the terminal ones *c.* 20-nerved, *c.* 11 cm long, 37 mm broad, long-acuminate at apex, acute, decurrent at base; the lateral ones *c.* 18–20-nerved, *c.* 6–9 cm long, 22–30 mm broad, acuminate at apex, acute to obtuse, decurrent at base; serrate at margin, very sparsely minutely strigose, glabrescent, or glabrous above and below; petiolule of terminal leaflets 8–10 mm, of lateral ones 4–6 mm long. *Inflorescences* axillary, paniculate, rather dense towards the extreme ramifications, many-flowered, *c.* 250 flowers or more, up to *c.* 12 cm long, 12 cm dia., the peduncle up to 3 cm long; branches generally more or less flattened, sparsely minutely strigose-hirsute at base to densely so in ultimate branchlets, with minute, early caducous bracts. *Flowers* with short (up to 0·5 mm long) pedicel, 4- or 5-merous. Sepals triangular-ovate, *c.* 1·7 mm long, 1·5 mm broad, short-strigose outside, densely so inside, glabrous along edge. Stamens with *c.* 0·8 mm long, terete (*c.* 0·1 mm dia.), near base slightly flattened, glabrous filament and obcordiform, *c.* 0·5 mm long, 0·4 mm broad, 0·3 mm thick, at apex faintly apiculate anther. Disk annular, *c.* 0·2 mm high, 0·4 mm broad, very densely short-hirsute. Ovary 4–5-celled, conical, *c.* 0·6 mm high, 0·5 mm dia., fairly densely short-hirsute; styles cylindrical, closely appressed, *c.* 0·2 mm long, 0·05 mm dia., glabrous except for few hairs near base. *Fruits* unknown.

Distribution.—North-eastern New Guinea, known only from the type collection.

2. **Aistopetalum viticoides** Schltr. in Bot. Jb. **52**: 144, fig. 2*A–F* (1914); Engl. in Engl. et Prantl, Nat. Pfl.fam., 2nd Ed. **18a**: 239, fig. 138*A–F* (1930); Perry in J. Arnold Arbor. **30**: 159 (1949). *Type specimen.—Ledermann* 12177, Schraderberg (NE. New Guinea), holotype in B.

Aistopetalum tetramerum Kan. et Hat. in Bot. Mag., Tokyo **56**: 105, fig. 1 (1942). *Type specimen.—Kanehira and Hatusima* 12803, Boemi, 45 km inward of Nabire (NW. New Guinea), holotype in FU (not seen), isotypes in A, BO.

Tall trees, up to *c.* 30 m high, 60 cm dia., with up to *c.* 12 m tall straight bole; bark blackish brown. Twigs rather distinctly flattened under the leaf pairs, the older ones terete; minutely strigose-puberulous, glabrescent. *Leaves* 1–2-jugate, lateral leaflets subopposite, occasionally unifoliolate. Stipules ovate-oblong, up to *c.* 7 mm long, 3 mm broad, densely minutely puberulous below. Petiole *c.* (10–)15–40 mm long, terete, flattened or shallowly channelled above, minutely strigose-puberulous; internodes of the rachis *c.* 10–25 mm long. Leaflets oblong, the terminal ones *c.* (10–)12–15-nerved, *c.* (3–)5–12 cm long, (12–)22–48 mm broad, the lateral ones *c.* (8–)10–14-nerved, *c.* (3–)4–11 cm long, (10–)18–42 mm broad; apex acute and acuminate, base acute to obtuse, long decurrent, unequal-sided in the lateral leaflets; margin shallowly crenate-serrate to subentire; sparsely puberulous, glabrescent, to glabrous above, fairly densely so to glabrous below; petiolule of terminal leaflets (4–)6–12 mm, of lateral ones (2–)3–7 mm long. *Inflorescences* axillary, paniculate, rather open and relatively few-flowered (up to *c.* 50 flowers), up to *c.* 9 cm long, 5 cm dia., the peduncle up to 3 cm long; branches generally more or less flattened, sparsely to densely puberulous, most densely so towards ultimate branchlets, more or less glabrescent, with minute, early caducous bracts. *Flowers* with up to 2·5 mm long pedicel, (4–)5–6-merous. Sepals ovate or triangular-ovate, *c.* 2·8–3·4 mm long, 1·7–2·6 mm broad, glabrous or sparsely short-strigose to densely strigose-hirsute outside, densely short-strigose, most densely so in central part, inside. Stamens with *c.* 1·7 resp. 1·4 mm long, terete (*c.* 0·1 mm dia.), near base flattened, glabrous filament and obcordiform, *c.* 0·8 mm long, 0·6 mm broad, 0·4 mm thick, at apex mucronate anther. Disk annular, *c.* 0·5 mm high, 0·6 mm broad, glabrous, with terebriform pattern. Ovary (4–)5–6-celled, conical, *c.* 1·2 mm high, 1·0 mm dia., with a row of hairs along outside centre of each cell; styles cylindrical, closely appressed, *c.* 0·4 mm long, 0·15 mm dia., glabrous. *Fruits* drupaceous, ovoid, *c.* 20 mm long, 13 mm dia., at apex with whorl of (4,) 5, or 6 protruding small horns around central depression; exocarp leathery, dark brown to black, slightly shiny, glabrous; endocarp woody, very hard; (4–)5–6-seeded, the seeds oblong, *c.* 6 mm long, 1·5 mm dia. (Fig. 6).

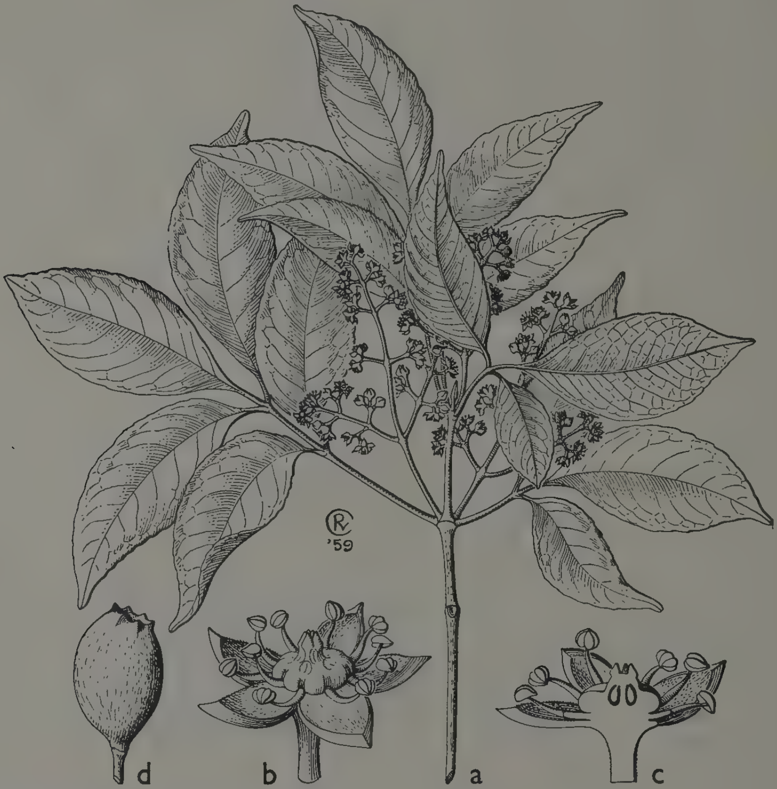

Fig. 6.—*Aistopetalum viticoides* Schltr. *a*, Flowering branch, × ½; *b*, open flower, ×5; *c*, longitudinal section of flower, ×5; *d*, fruit, natural size. (*a–d*, After *Hoogland and Pullen* 5883.)

Distribution.—Known from several localities in western (Arfak Mts.), north-western (Boemi, Bernhard Camp area), and north-eastern (Schrader Mt., Mt. Hagen) New Guinea, in primary forest from 300 to 2200 m altitude, most frequent in the 1000–2000 m zone.

Specimens Studied.—*Brass* 13286; *Brass and Versteegh* 12513, 12565, 13170; *Hoogland and Pullen* 5883; *Kanehira and Hatusima* 12803; *Kostermans* 2431; *Ledermann* 12128, 12177; *Womersley* NGF 9413.

A. tetramerum Kan. et Hat. was described as distinct by having 4-merous, rarely 5-merous flowers and ternate or rarely 5-foliolate leaves. 5-foliolate leaves are quite common in typical *A. viticoides* and are found even in the type specimen, though Schlechter described only 3-foliolate ones. An isotype of *A. tetramerum* in A with only young buds has several 5-merous flowers and it is hard to decide whether 4- or 5-merous ones predominate. It is certainly so that in other specimens examined tetramery is unusual and that in this character the specimen is aberrant, though in view of my observations on the isotype not to the same degree as Kanehira and Hatusima's description suggests. The basis for its acceptance as a distinct species appears to be insufficient, in particular since in all other characters the flowers agree perfectly well with *A. viticoides.* When more material, in particular fully grown flowers, becomes available it may be justified to give the form varietal rank, but at present I prefer to consider *A. tetramerum* synonymous with *A. viticoides.*

Kostermans 2431, distributed as *A. tetramerum,* has 5- and 6-merous flowers and fruits and represents a hirsute form of *A. viticoides.* In the nature of its indumentum the species appears to be rather variable. *Hoogland and Pullen* 5883 represents a nearly glabrous form, whereas the type and *Kanehira and Hatusima* 12803 are intermediate, the hairiness being mainly on the branches of the inflorescence, little on the outside of the sepals. *Kostermans* 2431 has the outside of the sepals with a dense strigose-hirsute indumentum; the leaves on this specimen are distinctly hirsute, whereas in all others they are glabrous or nearly so.

IV. GENUS CALYCOMIS D. Don

Calycomis Brown ex D. Don in Edinb. New Phil. J. **9**: 93 (1830); G. Don, Gen. Hist. **3**: 201 (1834); Meisn., Pl. Vasc. Gen. **1**: 138, **2**: 101 (1838); Endl., Gen. Pl. 818 (1839). *Type species.—C. verticillata* D. Don, only species ≡*C. australis* (A. Cunn.) Hoogl.

Acrophyllum Benth. in Maund., Bot. **2**: t.95 (1838); Benth., Fl. Aust. **2**: 443 (1864); Benth. et Hook.f., Gen. Pl. **1**: 652 (1865); Baill., Hist. Pl. **3**: 380, 452 (1872); Engl. in Engl. et Prantl, Nat. Pfl.fam. **3(2a)**: 100 (1891); Moore, Handb. Fl. N.S.W. 178 (1893); Engl. in Engl. et Prantl, Nat. Pfl.fam., 2nd Ed. **18a**: 246 (1930). *Type species.—A. venosum* (Knowles et Westcott) Benth., only species ≡*Calycomis australis* (A. Cunn.) Hoogl.

Shrubs with verticillate nearly sessile simple distinctly serrate leaves, with connate interpetiolar stipules with collaters; stipules with young leaves enclosing terminal bud, long-persistent; nerves and venation prominent on both sides, more strongly so below than above. *Inflorescences* in compact whorls, a series of whorls alternating with a series of whorls of leaves; each whorl consisting of 3 compact panicles in the axil of reduced leaves. *Flowers* 5-merous; sepals valvate; petals membranaceous, obovate-oblong; stamens 10, the episepalous ones very slightly longer than the epipetalous ones; filament filiform, terete, anthers dorsifixed, cordiform, ± entrorse with longitudinal slit; disk minute or absent; ovary superior, 2-celled, the cells partly free, each cell with *c.* 9–11 epitropous ovules; styles subulate, slightly divergent. *Fruits* 2-celled capsules, the carpels coriaceous, each with up to 6 seeds.

Distribution.—New South Wales, monotypic, restricted to a small area in the Blue Mountains.

The genus is easily characterized by the structure of the inflorescence and by the verticillate simple sessile leaves with subcordate base. In floral and fruit characteristics it comes very close to several other genera in the family, e.g. *Ackama, Weinmannia, Opocunonia,* and *Caldcluvia.*

The name *Calycomis* first appeared in R. Brown's "General Remarks, Geographical and Systematical, on the Botany of Terra Australis; Appendix to Flinders' Voyage", p. 549 (reprint: 17) (1814). He enumerates here the genera belonging to his new family ("order") Cunoniaceae. Very likely it is here an orthographic error for *Callicoma* Andr.; as it is a *nomen nudum*, it has no standing under the current code. D. Don was the first author to provide a description under the name and though he cited Brown as the authority for the genus his concept, and not Brown's, has to be followed. *Calycomis* (from Greek καλυξ = calyx and κομη = hair; cf. G. Don, loc. cit., 1834) cannot be considered an orthographic variant for *Callicoma* (from καλλος = beautiful and κομη). *Calycomis* D. Don antedates the currently used name *Acrophyllum* Benth. by 8 years and for this little-known genus conservation of the latter is not justified. *Calycomis* in the sense of *Callicoma* Andr. was first validly published as *Calycomis serrata* R.Br. ex Nees et Sinning, Samml. schönblüh. Gewächse t.29 (1831).

The name *Acrophyllum* was derived from the Greek ἀκροφυλος: "that has leaves at the top, in allusion to the tufts of leaves with which the flowering stems are crowned" (Benth., loc. cit., 1838).

1. **Calycomis australis** (A. Cunn.) Hoogl., comb. nov.

Weinmannia australis A. Cunn. in Field, Geogr. Mem. N.S.W. 353 (1825), reprinted in Linnaea **2**: 137 (1827); Ser. in DC., Prod. **4**: 9 (1830); G. Don, Gen. Hist. **3**: 198 (1834). *Type specimen.*—*A. Cunningham* s.n., Springbrook, New South Wales, lectotype in BM, possible isotypes in G, K.

Calycomis verticillata D. Don in Edinb. New Phil. J. **9**: 93 (1830); G. Don, Gen. Hist. **3**: 201 (1834); Walp., Rep. Bot. Syst. **5**: 828 (1846); F. Muell., Fragm. **6**: 189 (1868). *Type specimen.*—*Caley* s.n., New Holland, in Herb. Lambert, holotype now in BM, isotypes in A, E, W.

Weinmannia venosa Knowles et Westcott, Floral Cabinet **2**: 81, t.65 (1838); Walp., Rep. Bot. Syst. **2**: 373 (1843). *Type specimen.*—Probably a specimen in K.

Acrophyllum venosum (Knowles et Westcott) Benth. in Maund., Bot. **2**: t.95 (1838); Benth., Fl. Aust. **2**: 443 (1864); F. Muell., Fragm. **7**: 150 (1871); F. Muell. in Nuovo G. Bot. Ital. **3**: 30 (1871); F. Muell., Syst. Cens. Aust. Pl. **1**: 48 (1882); F. Muell., Sec. Syst. Cens. Aust. Pl. **1**: 82 (1889); Ch. Moore, Handb. Fl. N.S.W. 178 (1893); Pamp. in Ann. Bot., Roma **2**: 60 (1905); Maiden et Betche, Cens. N.S.W. Pl. 88 (1916).

Acrophyllum verticillatum (D. Don) Hook. in Bot. Mag. **69**: t.4050 (1843); Engl. in Engl. et Prantl, Nat. Pfl.fam. **3(2a)**: 100 (1891); Engl. in Engl. et Prantl, Nat. Pfl.fam., 2nd Ed. **18a**: 247 (1930).

Shrub *c.* 1–2 m tall. Twigs triangular when young, soon terete, glabrous or sparsely hirsute, early glabrescent, the older ones smooth with small leaf scars connected by narrow stipular scars; axillary buds, the scales with acute apices, commonly present. *Leaves* verticillate in whorls of 3 or occasionally opposite, decussate. Stipules subcoriaceous, narrowly triangular or triangular-ovate, *c.* 4–7 mm long, 1·5–2·5 mm broad, sharply acute at apex, entire or with few minute serrations at margin, with distinct midrib and some parallel nerves, sometimes splitting along midrib; glabrous or sparsely short strigose-hirsute below, glabrous above. Petiole *c.* 1–2 mm long, swollen in comparison with midrib, slightly grooved or flattened above, glabrous or sparsely short-hirsute. Blade ovate to ovate-oblong, *c.* (12–)16–20-nerved, *c.* 4–10 cm long, 18–45 mm broad; acute at apex, retuse or slightly cordate at base; margin deeply serrate with 1 or (only in lower part of leaf) 2 serrations per lateral nerve; venation reticulate; glabrous on intervenium and nerves, sparsely short-hirsute on midrib, with prominent nerves and venation, slightly sunken midrib above; often more or less glaucous, rather sparsely short strigose-hirsute on midrib, nerves, and venation, glabrous on intervenium, with prominent venation and very prominent midrib and nerves below. *Inflorescences* in compact whorls, (1–)3–5 whorls alternating with (1–)3–7 whorls of leaves, the individual whorls close together, thus the inflorescence-bearing part of the twig cylindrical, or at some distance from each other, thus the inflorescence-bearing part of the twig a series of globular inflorescence groups; growth of the twig continuous during flowering with whorl of young leaves already present when flowers only just opening and also frequently inflorescences and infructescences present separated by a vegetative part of the twig. Each floral whorl containing 3 (rarely 2) strongly reduced, early caducous leaves, 3 normal-sized, long-persistent stipules, and a compact panicle of up to *c.* 20 flowers in the axil of each leaf; dia. of floral whorl up to *c.* 2·5–3 cm. Central axis of panicle comparatively stout, *c.* 1·0 mm dia., the first branches very close to (<1 mm from) base; axis and branches sparsely short strigose-hirsute. *Flowers* with *c.* 2–5 mm long, terete, *c.* 0·2–0·3 mm, at apex up to 0·5 mm thick, sparsely hirsute pedicel. Sepals triangular-ovate to ovate-oblong, *c.* 2·2–3·0 mm long, 0·8–1·2 mm broad, acute, often with small gland, at apex, rounded at up to 0·8 mm broad base, fairly thin with rather distinct midrib and 2 less distinct parallel nerves, glabrous throughout or with very few hairs near base outside or along margin. Petals obovate-oblong, *c.* 2·8–3·5 mm long, 0·7–0·8 mm broad, obtuse to bluntly acute at apex, long-unguiculate at base, membranaceous with distinct midrib and usually a few lateral nerves, glabrous. Stamens

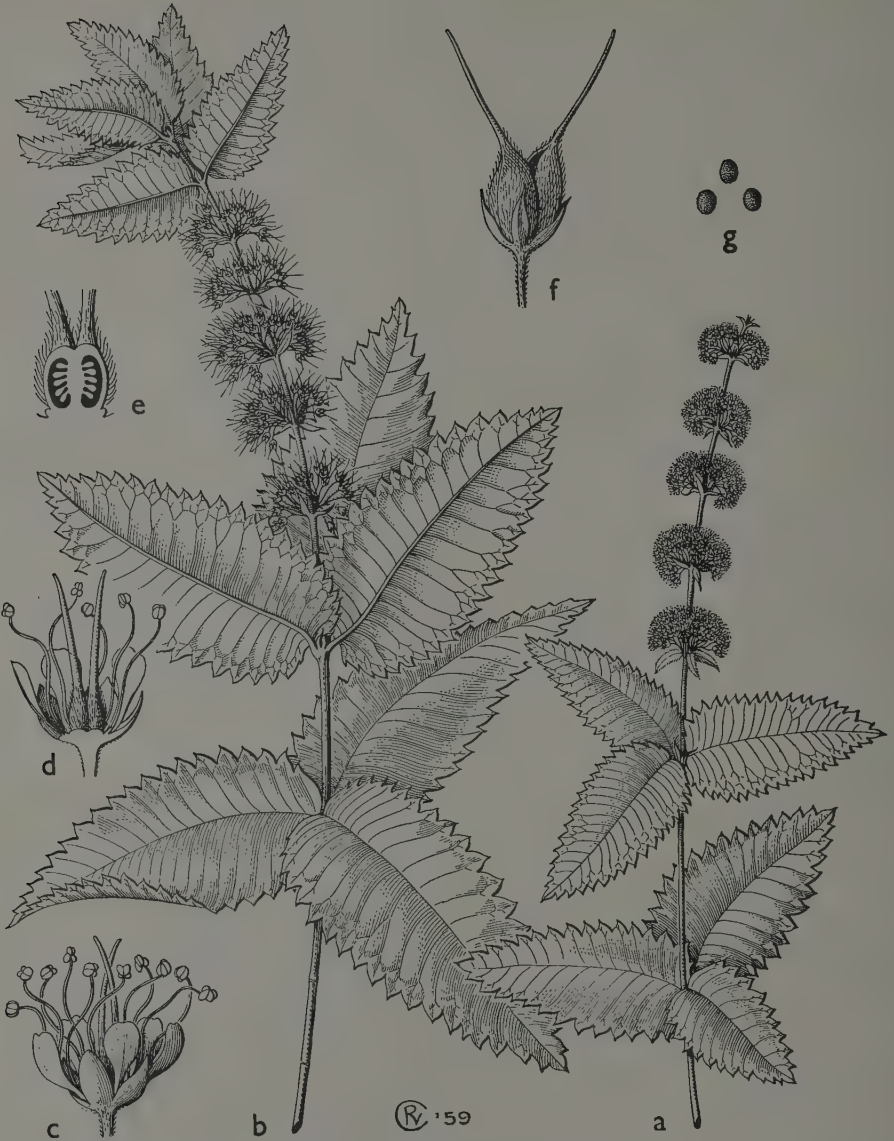

Fig. 7.—*Calycomis australis* (A. Cunn.) Hoogl. *a*, Flowering branch, $\times\frac{1}{2}$; *b*, fruiting branch, $\times\frac{1}{2}$; *c*, open flower, ×4; *d*, longitudinal section of flower outside the ovary, ×4; *e*, longitudinal section of ovary, ×10; *f*, fruit, ×4; *g*, seeds, ×4. (*a*, After "*d'Alleizette* 2158" (L); *b*, after *A. Cunningham* s.n. (GH); *c–e*, after *Constable* NSW 42305; *f*, *g*, as *b*.)

long exserted, the filament strongly curved in bud, in open flower up to 5·2 resp. 5·5 mm long; anther *c.* 0·5 mm long, 0·4 mm broad, 0·3 mm thick. Disk if at all distinct annular, up to 0·3 mm high, 0·05 mm thick, glabrous. Ovaries *c.* 1·2 mm long, 0·4–0·5 mm dia., the two attached for an area of *c.* 0·6 by 0·3 mm, strigose-hirsute with up to 0·4 mm long hairs; style glabrous or with a few strigose hairs near base, *c.* 3·5–4·0 mm long. *Fruits* with the calyx persistent; carpels *c.* 3·2 mm long, 1·9 mm broad, 1·0 mm thick, fairly sparsely strigose-hirsute; style *c.* 4·3 mm long, firm. Seed ellipsoid, *c.* 0·7 by 0·5 mm, with granular surface (Fig. 7).

Distribution.—Restricted to a small area in the Blue Mountains in New South Wales (Mt. Banks, Lawson, Woodford, Linden, Springwood), on moist shady rocks.

Specimens Studied.—*Caley* s.n.; *Constable* NSW 42305; *A. Cunningham* 28, 155, s.n.; *R. Cunningham* s.n.; *Hamilton* s.n.; *Maiden* s.n.; *Maiden and Cambage* s.n.; *Meebold* 3104; *Norton* s.n.; *Vermeulen* s.n.; *Walter* s.n.; *Weber* s.n.; *Woolls* s.n.; some specimens from cultivation.

THE AUSTRALIAN SPECIES OF *NICOTIANA* L. (SOLANACEAE)

By Nancy T. Burbidge*

[*Manuscript received March* 25, 1960]

Summary

Since the publication of the comprehensive account of the genus *Nicotiana* by Goodspeed and his collaborators (1954), extensive collecting by the author has revealed the existence of a number of undescribed species and has resulted in the compilation of data which allow a better understanding of specific relationships between those previously known.

In this paper the morphological characters by which species can be recognized are discussed, and five new species and two new subspecies are described. Two of the new species proved to have 23 pairs of chromosomes, thus filling a gap in the series of from 16 to 24 pairs which, with the exception of 17 pairs, has now been recorded for the Australian taxa. Notes on the relationships, the more important morphological features, and the geographical distribution are provided for all previously recognized species.

Introduction

The Australian species of *Nicotiana* L. are all members of the section *Suaveolentes* (Goodspeed 1945) which is almost wholly restricted to the Australian continent. One species, *N. debneyi* Domin, is also found on Lord Howe Island and in New Caledonia; and one species, *N. fragrans* Hook., which occurs on certain islands of the Pacific, is distinct from the Australian taxa in having a perennial habit and is the only non-Australian species in the *Suaveolentes*.

The most important works dealing with the Australian species are the book published by Goodspeed (1954) and an earlier paper by Wheeler (1935). In the taxonomic portion of Goodspeed's book (prepared by Goodspeed, Wheeler, and Hutchison but for brevity quoted here as "Goodspeed") the *Suaveolentes* are placed in the subgenus *Petunioides* and distinguished by the non-deflexed corolla limb, by the corolla throat not or only slightly dilated, and by the fact that the lowest anther is on the longest filament (except in *N. debneyi*). The *Suaveolentes* are regarded as having affinities with the South American sections *Alatae*, *Noctiflorae*, and *Acuminatae*. The characters suggesting such relationships are shown in differing combination in the various Australian species.

The identification of specimens of *Nicotiana* in Australia is made difficult by the range of variation sometimes exhibited. Such variations may be due to habitat, e.g. when conditions are dry and the leaves are restricted to the basal rosette and the panicle is reduced to a subsimple raceme. Flower size varies with the vigour of the plant and with maturity. Early and late flowers are usually smaller than those produced at the full flush of anthesis. As might be anticipated, the humid conditions of a greenhouse also result in deviations from the typical habit of field specimens in many cases.

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Experience has shown that the drawings, descriptions, and key provided in Goodspeed's book are based on fresh material grown under cultivation in conditions better than those from which the majority of field and herbarium specimens come. Thus his key, though based on a satisfactory range of characters, is not always easy to employ when one is restricted to dried plants.

Since 1955 the author has made a number of field trips to obtain native species of *Nicotiana*. The material collected, as herbarium specimens, as transplants, or as seed samples, is being used in studies into disease resistance carried out by other officers of the C.S.I.R.O. The areas visited include northern Australia, the drier areas of Western Australia, central Australia, South Australia, and western and southern Queensland.

The Australian species have marked habitat preferences. They are usually associated with disturbed areas, such as recent regrowth on burnt patches or along newly made country roads or places where competition from other plants, especially perennials, is limited. A number of species occupy sites shaded from the heat of the midday and afternoon sun, as in the case of three of the new species described in this paper. Plants are rarely found in "closed" communities of perennial species, though they do occur amongst the flush of ephemerals following rains in arid areas, and in such communities are always best developed in the shade of shrubs and trees.

In addition to plants examined in the C.S.I.R.O. Herbarium or observed in the glass-house and the field, the author has examined specimens from the herbaria at Brisbane, Sydney, Melbourne, Adelaide, and Perth. Some of the sheets are quoted in the notes under the various species but comprehensive lists are provided only in the cases of new species. The remainder may be consulted at the respective institutions.

Full descriptive notes are not provided where the species are distinctive, where they are well described by Wheeler and by Goodspeed, or where they can be readily determined by the characters in the key. The notes provide comments on the principal diagnostic characters and the geographic distribution.

Morphological Characters of Diagnostic Significance

General Habit.—Growth habit is not always evident in herbarium material, though where available it may be helpful, as in cases where the cauline leaves are or are not well developed. This character must be used with discretion, since plants from favourable sites or from the glass-house almost always have a higher number of cauline leaves than is usual in field specimens. For example, *N. megalosiphon* Heurck & Muell. Arg., as seen in glass-house plants or plants from the higher-rainfall areas of eastern Queensland, has leafy stems and few persistent basal leaves, but plants from arid habitats in western Queensland or central Australia may have most of the leaves in the basal rosette. In *N. exigua* Wheeler and *N. goodspeedii* Wheeler the majority of the leaves are in the basal rosette but the number of stem leaves increases under better conditions. In *N. rosulata* (S. Moore) Domin all or almost all leaves are in the basal rosette, though on secondary regrowth the stem may have a few leaves if growing under moist conditions.

Leaves.—Throughout the key it is the shape of the cauline leaves which has been used for diagnostic purposes. The chief reason for this is that such leaves are more likely to be present on herbarium specimens. In general the cauline leaves show a progression from the shape of the radical leaves to those which pass into the commonly minute bracts of the inflorescence. Thus in *N. occidentalis* Wheeler the basal leaves are obtusely spathulate with long strap-like bases. The lower cauline leaves have shorter stem-clasping bases and narrower apices, and the upper ones become lanceolate or linear. The larger the plants the more numerous are the auriculate cauline leaves, though in many field specimens these may not be conspicuous.

Flowers.—Size of flower is notoriously variable in *Nicotiana*, and may be affected by the stage of maturity of the plant and by the length of day as well as, to a lesser extent, the vigour of the plants (see above). Under short-day conditions the flowers of some species become cleistogamous, in which case the corolla may barely exceed the calyx. Familiarity with a number of species permits a proper allowance for such deviations, but in most cases the gross differences in flower size may be used for diagnostic purposes.

In general flowers fall into two main classes. In one the tube is relatively broad and the limb diameter is rarely more than three times that of the tube. In the other group the tube is slender and much longer than wide, and the spreading limb is well formed. In Goodspeed (1954) the corolla is considered as consisting of the "tubular part" and the limb. The tubular part is deemed to include: (1) the "tube proper", which is "the narrowest basal portion"; (2) the rest of the tubular part; (3) the throat, which is "the upper part of the tubular part". In practice the application of these terms to the Australian species is not always easy. In particular the base of the tube proper is usually expanded over the young capsule in herbarium specimens. For this reason the anatomical significance of the various parts of the corolla tube has been ignored, and the term "tube" is applied to all parts below the spreading limb, including the "throat", which is that part which surrounds the upper stamens. Relative proportions of the tube are used in the key. Throat shape is only important where there is asymmetry due to subdidynamy of the upper stamens.

In many species the corolla lobes are shallow and emarginate. In *N. benthamiana* Domin, *N. gossei* Domin, and in *N. cavicola* sp. nov. they are obtuse, in *N. umbratica* sp. nov. they are acute, and in *N. excelsior* J. M. Black they are so shallow as to be almost absent. In some species the limb is reflexed on one side, as in *N. debneyi* and in *N. rotundifolia* Lindl. (Plate 7), but this character is more readily seen in fresh material than in herbarium specimens, and has therefore been omitted from the key.

Except in *N. debneyi*, the stamens are arranged with four anthers on short equal or unequal filaments in the throat and one on a longer filament attached lower in the tube. In species where the upper stamens have unequal filaments there is a tendency to subdidynamy, i.e. one pair is placed slightly above the other. In *N. occidentalis* subsp. *obliqua* subsp. nov. and in certain related species this pairing of the upper stamens results in some asymmetry of the throat and a bending to one side of the limb, a character used in Goodspeed's key. The characteristic appearance of the corolla in both buds and flowers which results from this (Plates 8, 9) is best seen in fresh material, but is discernible in the buds of dried specimens provided they have been pressed from a suitable angle. If not the flower must be dissected to observe the staminal arrangement.

Capsule.—The shape of the capsules varies from broadly ovoid to narrowly ellipsoid, but is rarely highly distinctive. The placenta is relatively constant and of no diagnostic value.

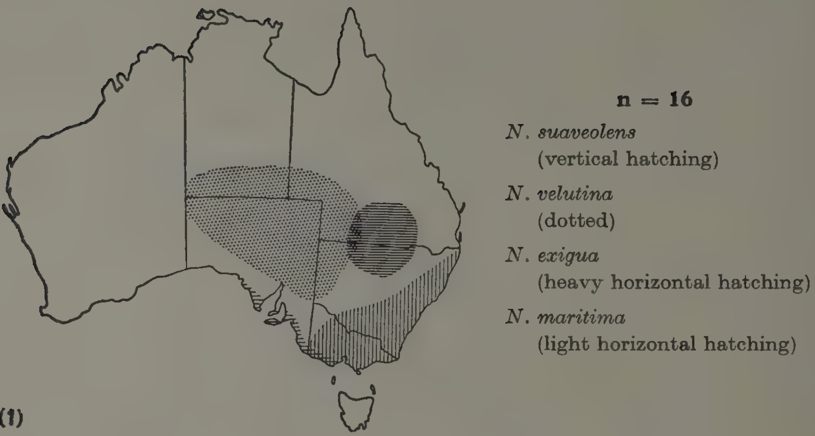
Seeds.—The shape of the seeds and the texture of the testa pattern do not seem to have been previously used for diagnostic purposes, but within the Australian species these features have proved most useful. Though similar patterns occur in different species these rarely occur in the same locality. The seed character is best applied where comparative samples are available, but despite this proviso the characters are valuable. Thus in small specimens of *N. velutina* Wheeler, undersized flowers may suggest that the specimen belongs with *N. rotundifolia*; but in the former species the seeds are strongly curved (C-shaped) and the surface has a reticulation of serpentine wrinkles, whereas in *N. rotundifolia* the seeds are only slightly curved and are broader at one end, while the reticulations are of an irregular honeycomb pattern with fluted ridges radiating from the micropyle. (Plates 10–20.)

Seeds with serpentine or undulate reticulation generally have round-edged wrinkles, whereas in those with honeycomb reticulation the ridges are sharply raised so that in profile the seed may even appear submuricate. In young seeds the spaces between the ridges may appear speckled owing to large epidermal cells. These are of no diagnostic value and usually disappear in the darker mature seeds.

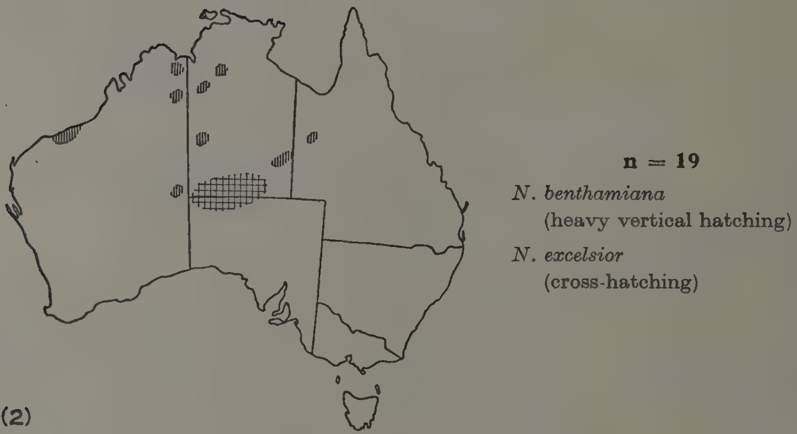
Vestiture.—Another useful character is that of the type of hairs present on the epidermis. The types have been described by Goodspeed (1954) but for general diagnostic purposes only a few are of special interest. Those present vary from species to species and also from organ to organ of the plant. To avoid confusion it should be understood that references used in the key in this paper concern hairs to be found on the pedicels and calyces unless it is clearly stated otherwise.

The two main types of glandular hairs are the most useful for diagnostic purposes. In one the multicellular hair terminates in a single globular apical cell, and the plants are commonly moist or slightly viscid when fresh. In the other the hair has an ellipsoid head of numerous minute cells whose divisions are not all at right angles to the axis of the trichome. In species having this type, the plants are viscid to the touch and there are usually fragments of material adherent to the specimen. These ellipsoid heads sometimes darken with age or with adherent dust, and they may then be visible to the naked eye. To ascertain which type of hairs is present on the pedicels and calyces it is desirable to soak them in water or a weak solution of "Teepol" or other detergent, since otherwise the secretion may obscure the apices of the trichomes.

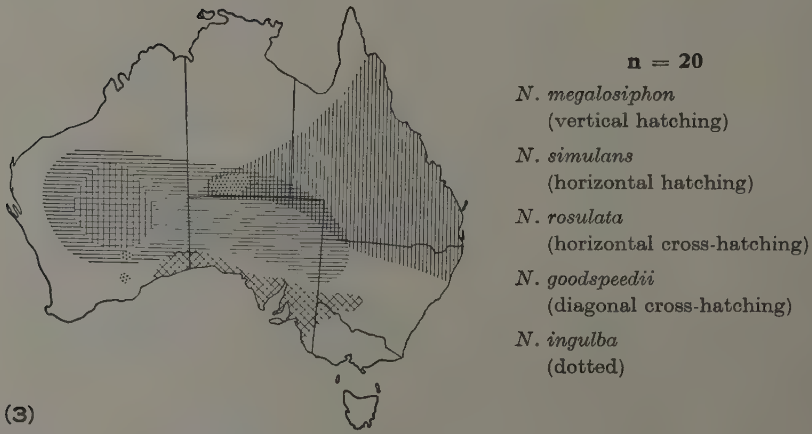
The simple globular type may be seen in *N. megalosiphon*, *N. simulans* sp. nov., and *N. gossei* Domin (see Fig. 12*D*, *E*, *G*). In all these the variation in trichome length is more marked than in species bearing the second type. The ellipsoid-headed


n = 16
N. suaveolens
(vertical hatching)
N. velutina
(dotted)
N. exigua
(heavy horizontal hatching)
N. maritima
(light horizontal hatching)

(1)


n = 19
N. benthamiana
(heavy vertical hatching)
N. excelsior
(cross-hatching)

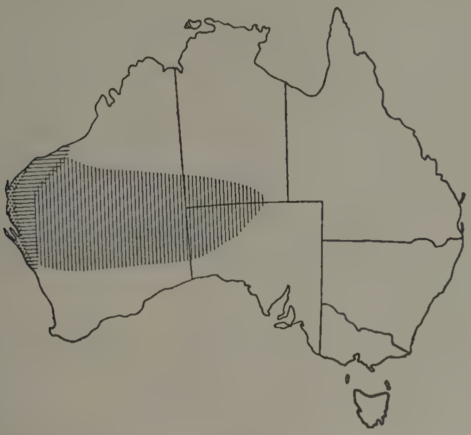
(2)


n = 20
N. megalosiphon
(vertical hatching)
N. simulans
(horizontal hatching)
N. rosulata
(horizontal cross-hatching)
N. goodspeedii
(diagonal cross-hatching)
N. ingulba
(dotted)

(3)

Figs. 1–3.—Maps indicating distribution of species of different chromosome numbers (n).

type may be seen in *N. occidentalis* (both subspecies), *N. debneyi* (see Fig. 12*C*, *F*), *N. benthamiana*, *N. cavicola*, and *N. umbratica*. In these species the specialized glandular trichomes may be the only type present on the pedicels and calyces, or there may be a few small simple trichomes which suggest an immature condition. Even the hydathodes (Fig. 12*A*, *E*) may be very few in number.



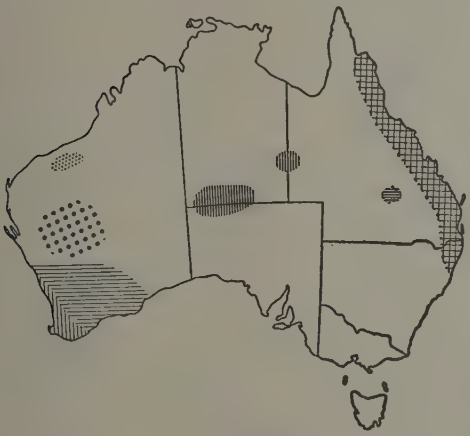
n = 21

N. occidentalis subsp.
occidentalis
(horizontal hatching)

N. occidentalis subsp.
obliqua
(vertical hatching)

N. hesperis
(dotted)

Fig. 4.—Map indicating distribution of species in the *N. occidentalis* complex (subsp. *obliqua*).



N. debneyi (*n* = 24)
(cross-hatching)

N. umbratica (*n* = 23)
(small dots)

N. cavicola (*n* = 23)
(large dots)

N. rotundifolia subsp.
rotundifolia (*n* = 22)
(light vertical hatching)

N. rotundifolia subsp.
aridicola (*n* = 22)
(light horizontal hatching)

N. gossei (*n* = 18)
(heavy vertical hatching)

N. amplexicaulis (*n* = 18)
(heavy horizontal hatching)

Fig. 5.—Map indicating the distribution of the following species: *N. debneyi*, *N. umbratica*, *N. cavicola*, *N. rotundifolia* subspp. *rotundifolia* and *aridicola*, *N. gossei*, and *N. amplexicaulis*.

Branched hairs with globular apical cells have been found in *N. rotundifolia* subsp. *rotundifolia*, this being the first record of their occurrence in any member of the *Suaveolentes*. Long once-branched hairs occur among simple hairs on the pedicels (Fig. 12*A*), and short, once- or twice-branched hairs may be present towards the apices of the calyx lobes (Fig. 12*B*). Such branched hairs were found on both field and glass-house specimens, but were not observed on the main stem or the leaves. They appear to be absent from *N. rotundifolia* subsp. *aridicola* subsp. nov.

Distribution and Intraspecific Relationships

The distribution of the Australian species is indicated in a generalized manner in Figures 1–5.

Goodspeed postulates that *Nicotiana* reached Australia by an Antarctic route, and that *N. suaveolens* ($n = 16$) (Fig. 1) and *N. debneyi* ($n = 24$) (Fig. 5), which are both restricted to eastern and south-eastern Australia, represent the modern forms of the original migrants. Other species are believed to have developed as a result of hybridization and introgression.

As might be expected, if this is correct, species with 20 pairs of chromosomes (Fig. 3) form the largest group and include the most widespread. Three of these species, *N. rosulata*, *N. ingulba*, and *N. goodspeedii*, all show close morphological relationships with *N. suaveolens*. The remaining two, *N. megalosiphon* and *N. simulans*, are less obviously linked with either *N. suaveolens* or *N. debneyi*, but *N. simulans* is morphologically intermediate between *N. megalosiphon* and *N. occidentalis* subsp. *obliqua* ($n = 21$) (Fig. 4).

N. rotundifolia (Fig. 5) is the only species recorded as having 22 pairs of chromosomes. The count was originally made on material now placed with subsp. *aridicola*. Morphologically the two subspecies are linked with *N. velutina* and *N. maritima* (both $n = 16$) (Fig. 1).

N. occidentalis (on a count for subsp. *obliqua*, $n = 21$), *N. benthamiana* ($n = 19$), *N. cavicola*, and *N. umbratica* ($n = 23$) not only have higher chromosome complements but reveal affinities with *N. debneyi* through the development of specialized glandular trichomes on the epidermis.

N. exigua ($n = 16$) is closely similar to *N. goodspeedii*. *N. gossei* and *N. amplexicaulis* sp. nov. (both $n = 18$) (Fig. 5) have restricted distributions. The former shows some affinities with *N. megalosiphon* and possibly *N. occidentalis*, though specialized glandular trichomes are absent. *N. amplexicaulis* appears to lie between *N. gossei* and *N. debneyi*, having the habit of the former and the flower shape of the latter. *N. excelsior* ($n = 19$), like *N. ingulba*, is only found in central Australia. It exhibits characters linking it with *N. suaveolens*, but the slender flowers suggest an affinity with *N. megalosiphon*.

The situation may be summarized by saying that species with higher numbers of chromosomes are found in the western, north-western, and eastern portions of the continent, those with $n = 20$ dominate the central areas, and those with $n = 16$ are found from central Australia to south-eastern Australia.

Key to the Australian Species of Nicotiana

A. Cauline leaves broadly ovate, cordate, or rhomboid, commonly as broad as long and abruptly narrowed into a slender or winged petiole. Stem-clasping auricles absent
  B. Cauline leaves, or at least the lower ones, with slender petioles which may be as long as the laminae
    C. Upper cauline leaves sessile and forming leafy bracts. Laminae ovate to broad lanceolate, obtuse. Corolla lobes obtuse .... 1. *benthamiana*
    C. Cauline leaves never forming sessile leafy bracts. Laminae cordate with deep basal sinus. Corolla lobes acute .... 2. *umbratica*

B. Cauline leaves with winged petioles and undulate laminae, upper ones narrower and associated with early flowers, later flowers with minute narrow bracts. Corolla lobes obtuse ....3. *cavicola*

A. Cauline leaves (if present) pandurate, spathulate, ovate, lanceolate, or elliptical but always longer than broad; sessile decurrent or narrowed into a short petiole, sometimes auriculate and stem-clasping. Inflorescence without leafy bracts

D. All stamens on slender filaments attached low in corolla tube. Seeds only slightly curved and with highly serpentine reticulated markings ....4. *debneyi*

D. Upper four stamens on short filaments in the throat or upper part of tube, fifth placed lower but on longer filament

E. Plants villous or pubescent with numerous soft woolly or glandular hairs (of various types) on all parts

F. Flowering calyx more than 16 mm long, intersepal membranes short. Corolla tube villous, 40–90 mm long. Seeds slightly curved and with sharply raised serpentine reticulation. Plants villous ....5. *gossei*

F. Flowering calyx less than 16 mm long, or if more then corolla not villous. Plants pubescent, puberulent, or with sticky glandular hairs

G. Corolla tube less than 10 times as long as its diameter at top of calyx. Calyx lobes lanceolate with short intersepal membranes

H. Cauline leaves pandurate with stem-clasping auricles. Seeds almost straight, the reticulum of deep rounded wrinkles. Corolla lobes obtuse ....6. *amplexicaulis*

H. Cauline leaves not auriculate. Corolla lobes emarginate

I. Plants pubescent to subvillous, leaves sessile or with winged petioles. Seeds slightly curved and with sharply raised honeycomb reticulation .... 7. *maritima*

I. Leaves puberulent or velvety, narrowed below into short petioles. Seeds strongly curved and with serpentine reticulation ....8. *velutina*

G. Corolla tube slender and at least 8 times as long as its diameter at top of calyx. Calyx lobes linear-subulate or linear-lanceolate, intersepal membranes extending almost to base of tube

J. Plants with ellipsoid-headed glandular hairs (especially on pedicels and calyces) Stems leafy

K. Seeds bent into tight U-shape, sometimes dorsally crested, reticulation forming transverse wrinkles. Corolla tube less than 35 mm long, throat straight ....9. *hesperis*

K. Seeds turgid, curved or reniform (C-shape), reticulation slightly serpentine with rounded ridges. Corolla tube more than 30 mm long

L. Corolla tube not bent at throat, limb symmetrically flared ....10. *occidentalis* subsp. *occidentalis*

L. Corolla tube asymmetrically flared at throat owing to subdidynamous upper stamens, limb slightly bent to one side..11. *occidentalis* subsp. *obliqua*

J. Plants without ellipsoid-headed glandular hairs, the trichomes varying in type and length, the glandular ones terminating in a simple globular cell. Cauline leaves sometimes absent or few

M. Corolla tube more than 25 mm long. Seeds flattened at broader end, with sharply ridged honeycomb reticulation

N. Corolla tube usually less than 30 mm long (25–40 mm), 1–1·5 mm diameter at top of calyx, asymmetrical at throat around subdidynamous upper stamens, limb not constricted above stamens ....12. *simulans*

N. Corolla tube more than 40 mm long (40–90 mm), 1·5–2 mm diameter at top of calyx, the throat symmetrically swollen about the subsessile upper stamens and slightly constricted at the base of the limb until late bud stage ....13. *megalosiphon*

M. Corolla tube less than 20 mm long, upper stamens not subdidynamous, limb not oblique in bud. Seeds curved or reniform

O. Reticulation of testa of honeycomb type. Calyx lobes lanceolate-acuminate, stems leafy ....14. *rotundifolia* subsp. *rotundifolia*

O. Reticulation of testa with serpentine markings. Calyx lobes linear or linear-subulate, the intersepal membranes pale and conspicuous leaves mainly or all basal ....15. *rotundifolia* subsp. *aridicola*

E. Plants almost or quite glabrous, or with loose spreading hairs on lower part of stems and glabrous above (glandular hairs always present on pedicels and flowers)

P. Cauline leaves decurrent. Calyx more than 15 mm long. Corolla limb almost entire, the lobes not emarginate, tube slender and 30–50 mm long. Seeds slightly curved and with honeycomb reticulation of sharply prominent ridges ..16. *excelsior*

P. Cauline leaves not decurrent, sometimes absent or few. Corolla lobes emarginate

Q. Corolla tube broad in proportion to its length, 3–5 mm diameter at top of calyx, 20–45 mm long. Calyx 10–25 mm long. Seeds slightly curved with serpentine round-edged wrinkles forming the reticulation ....17. *suaveolens*

Q. Corolla tube slender, less than 3 mm diameter at top of calyx. Seeds curved into C-shape

R. Stems leafy, or if leafless then either wholly glabrous or with sparse soft hairs on younger parts. Capsule 2–3½ times as long as broad. Seed reticulation of round-edged serpentine wrinkles

S. Corolla tube slender, more than 20 mm long with well-developed limb, upper stamens often subdidynamous. Stem leaves elliptical or ovate-lanceolate. Seed curvation not tightly reniform ....18. *ingulba*

S. Corolla tube less than 20 mm long, limb diameter rarely more than 2–3 times that of tube. Seeds reniform and tightly curved so that ends may touch, reticulation fine-grained

T. Capsule ovoid. Cauline leaves elliptical with minute soft hairs on margins and main veins ....19. *exigua*

T. Capsule oblong. Cauline leaves oblanceolate, glabrous or rarely with two or three distant marginal hairs ....20. *goodspeedii*

R. Stems leafless and with conspicuous spreading hairs in lower part though completely glabrous above apart from the glandular pubescence of the pedicels and flowers. Capsule narrow ellipsoid, 5–6 times as long as broad. Seeds almost straight and with sharply raised honeycomb pattern of sub-serpentine ridges ....21. *rosulata*

1. **Nicotiana benthamiana** Domin in Bibl. Bot., Stuttgart **89**: 591, pl. 37, fig. 1 (1929); *N. suaveolens* var. *cordifolia* Benth., Fl. Austral. **4**: 470 (1868); Goodspeed, Genus *Nicotiana* 485 (1954).

Holotype.—"N.W. Coast", *Bynoe* (collected during the voyage of the *Beagle* under the command of Wickham and Stokes) (K).*

A considerable range of variation is at present accepted under this name, as can be seen by a comparison of Domin's figure with that published by Goodspeed.

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* Abbreviations for the various herbaria are given in accordance with the list published in the "Index Herbariorum", third edition (1956).

Study of the material available has revealed that differences between specimens are in part due to whether the plants were collected in a juvenile, mature, or secondary regrowth state as well as to differences between populations. The population variations show characters occurring in different combinations and there is too little evidence on which to attempt any subdivision. At the same time, since this variation is present, it is desirable to recognize which form is represented by the holotype.

A photograph of the Bynoe specimen, held in the herbarium of the Royal Botanic Gardens, Kew, has been kindly made available by the Director of that institution and is shown in Plate 1. It consists of six pieces in which the leaves are all sessile, and which evidently represent the ends of flowering shoots, and one piece which is less floriferous and which bears petiolate leaves. There are indications that Domin's figure was based on more than one of these pieces. Domin also quoted with his description a Clement specimen, from the Pilbara area of Western Australia, and a photograph of this, also received from Kew, is shown in Plate 2. The sheet bears a robust shoot of *N. benthamiana* with petiolate leaves and also a piece representing *N. occidentalis* Wheeler. The reader should compare the specimens of *N. benthamiana* on these two Kew sheets with the glass-house plants shown in Plates 3 and 4. In Plate 3 the plant illustrated was grown from seed of transplants collected near the Ord River, Kimberley Division of Western Australia (T.S. 299). Plate 4, Figure 1, shows a plant grown from seed of transplants from Mundabullangana Station, south of Port Hedland, Pilbara district, Western Australia (T.S. 318), and hence topographically related to the Clement specimen; and Plate 4, Figure 2, shows a plant grown from seed received from the United States as *N. benthamiana* (C.P.I. 21181) and evidently closely resembling that figured by Goodspeed.*

It will be noted that the first flowers appear on the main shoot and are rarely truly axillary (cf. the Clement sheet). At a slightly later stage axillary flowering shoots develop. If these arise in the upper axils they have the appearance of the sessile-leaved pieces on the Bynoe sheet, but if they are from the lower axils the leaves are petiolate and comparable to the piece in the lower centre of the Bynoe sheet.

The original transplants for T.S. 299 were very undersized and less than 10 cm high. Under glass-house conditions the secondary regrowth on these consisted of numerous short shoots of the "basal" type, but in second generation plants (Plate 3) a strong main shoot dominates the growth. In other forms the robust main shoot is normal and basal shoots are usually poorly developed. Branching as shown in C.P.I. 21181 is not common in other samples. Since robust plants may be more than 1 metre high the range of size, type of branching, and position of the branches collected will have a strong effect on the appearance of a particular herbarium specimen.

In the Bynoe specimen, T.S. 299 and T.S. 318, the sessile leafy bracts are ovate to broadly lanceolate, whereas in C.P.I. 21181 and also in Goodspeed's figure they are obovate to oblanceolate. In all specimens the calyx is very loose about the base of the corolla, but in T.S. 299 and T.S. 318 the calyx lobes appear spathulate owing to the incurving of the lower margins, while in C.P.I. 21181 the lobes are conspicuously recurved and the margins are flat. In T.S. 299 the seeds have a honeycomb type of reticulation of the testa, but in all the other specimens examined the markings of the reticulation are undulate-serpentine, though the pattern is of the honeycomb type. (Plate 10.) According to information kindly provided by Dr. R. Melville, at Kew, the seeds of the Bynoe specimen agree with those of T.S. 299; and for this reason, plus the closer morphological resemblance and the geographical relationship, it is believed that T.S. 299 is the nearest to the type.

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* The letters T.S. (Tobacco Seed) and C.P.I. (Commonwealth Plant Introduction) refer to seed series held by the C.S.I.R.O.

Among other specimens examined, *Chippendale* 4550, from the Rawlinson Ranges on the Western Australian/central Australian border, is a very immature plant with "basal shoot" habit. *Perry* 2269, from 40 miles west of Wave Hill Police Station, Northern Territory, and *Lazarides* 6292, from 15 miles north-east of Hall's Creek, Kimberley Division, W.A., are similar to T.S. 299 except in seed coat reticulation; while *Perry* 5556 from 10 miles south-west of Tarlton Downs (grown at Canberra as T.S. 139), *Chippendale* 1799 from near Alcoora Springs, Tobermorey Station (both in the south-west of the Northern Territory), and material grown under T.S. 87 from seed collected by Greenway on Kallala Station, Dajarra, western Queensland, all represent robust plants but combine some of the characters observed in T.S. 318 with some of those in C.P.I. 21181. Distribution is shown in Figure 2.

All samples tested, viz. T.S. 299, T.S. 318, T.S. 139, and C.P.I. 21181, had 19 pairs of chromosomes.

These remarks may be summed up by stating that, provided allowance is made for the variations discussed here and shown in the plates and figures, the descriptions provided by Wheeler (1935) and by Goodspeed (1954) are satisfactory.

2. **Nicotiana umbratica** sp. nov.

Holotype.—Woodstock Station, Pilbara district, W.A., *E. H. M. Ealey*, E.161, received Canberra May 1958 (CANB).

Herba annua, glanduloso-pilosa. *Folia* petiolata, petioli longi graciles, laminae cordatae acuminatae rare obtusae, margines integrae. *Inflorescentia* sparse paniculata bracteata, bractea lineares, pedicelli 6–18 mm longi. *Calyx* angularis 10–16 mm longus, lobi lanceolati, recurvi. *Corolla* alba; tubus 45–65 mm longus, limbus 20–35 mm diametro, lobi ovati acuti. *Stamina* inclusa, quattuor adnata, quintum brevius semiadnatum. Stigma inclusum vel exsertum. *Capsula* ovoidea, calyce persistenti brevior. *Semina* brunnea vel fusca, testa undulato-reticulata.

An annual branched herb viscid with ellipsoid-headed glandular hairs on all parts, the hairs variable in length. *Leaves* with slender petioles often as long as or longer than the broadly ovate laminae, whose basal lobes are rounded and sometimes large enough to overlap in the median line (in fresh material), and whose apices are usually slender and acuminate (rarely obtuse). There is little difference between the leaves in different parts of the stems. *Inflorescence* subracemose or paniculate, commonly formed of several racemes terminating the leafy branches and their axillary shoots. *Calyx* 10–15 mm long, the tube angular on the intersepal

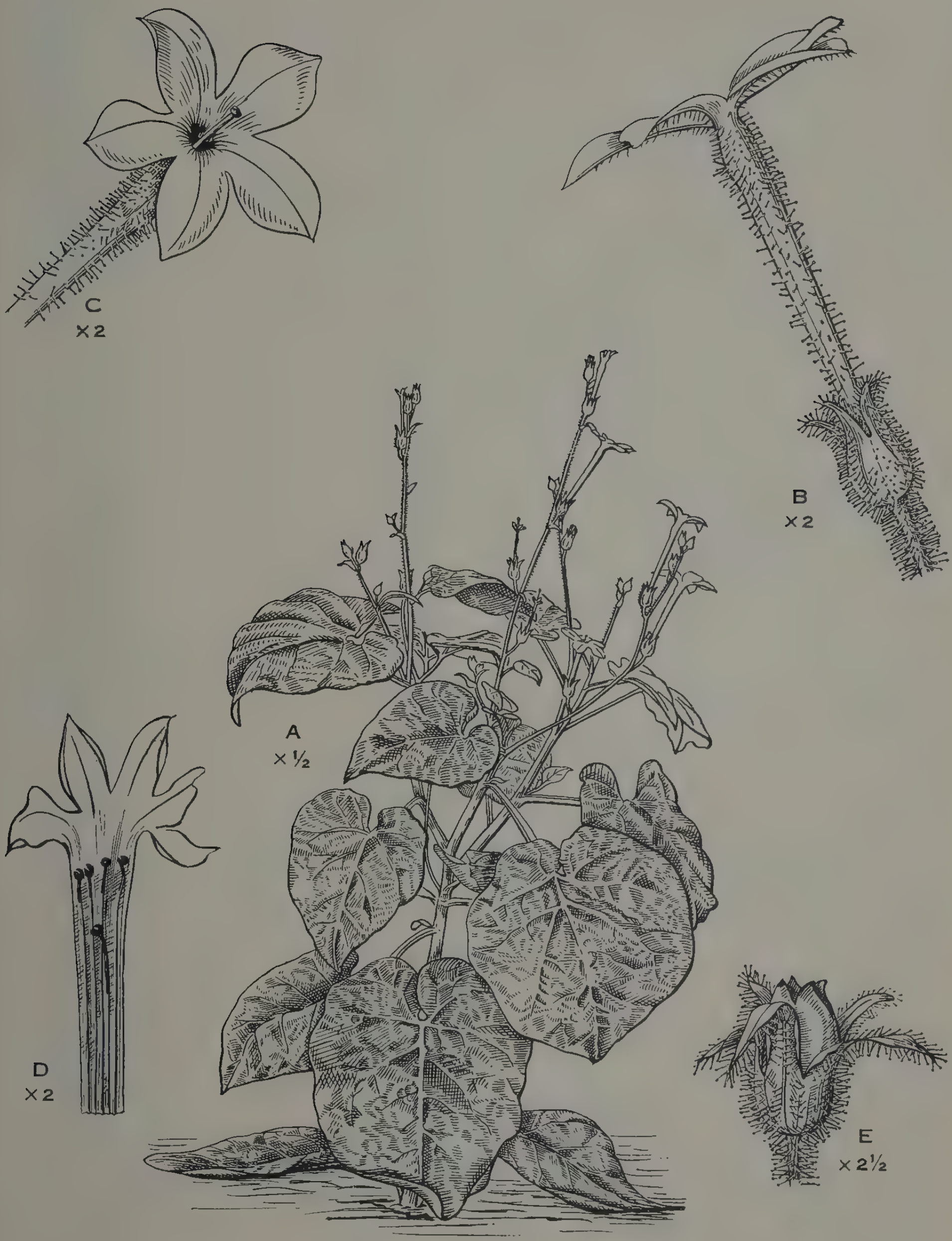

Fig. 6.—*N. umbratica* sp. nov. (drawn from glass-house plant of T.S. 301 = *Burbidge* 5820). *A*, plant; *B*, flower; *C*, corolla; *D*, corolla tube from within; *E*, calyx and capsule.

membranes and the prominent nerves, obtuse at the base and loose about the narrow corolla tube; lobes about as long as the tube but subequal in length, lanceolate, and usually recurved in fresh material. *Corolla* white, the glandular hairs continued along the mid nerve of each lobe; tube 45–65 mm long, throat 3–4 mm in diameter when flattened, slightly swollen around the anthers and constricted above them, limb 20–35 mm in diameter, the lobes ovate and acute, the mid nerve green and pilose below. *Stamens* included, 4 almost wholly adnate apart from short filaments below the anthers which lie slightly below the opening of the throat, the fifth shorter but with a longer partially free filament. *Style* sometimes long, so that the stigma is 1–1·5 cm above the throat, but more usually about as long as the upper stamens. *Capsule* ovoid, shorter than the persistent calyx. *Seeds* brown or dark brown, the testa marked with reticulate undulate wrinkles. Chromosome number 23 pairs. (Fig. 6; Plate 11, Fig. 1.)

The majority of the specimens examined were from the glass-house but the seed samples and transplants are represented by herbarium specimens collected in the field. The species is common in the Woodstock-Abydos area of the Pilbara district in the north-west of Western Australia (Fig. 5). So far as is known it is always associated with rock outcrops. It has been given its specific epithet because it normally grows under the shade of large boulders where it is protected from much of the heat of the sun. Notes on the ecology of its habitat have been published recently (Burbidge 1959).

Specimens Examined

Field specimens.—Woodstock-Abydos, *E. H. M. Ealey*, Feb. 1958 (cf. T. S. 298) (CANB): Abydos, S. of Port Hedland, in friable soil in cool shelter under large rocks, *N. T. Burbidge* 5873, 26.iv.1958 (cf. T.S. 303); "Ram Granite", Woodstock, S. of Port Hedland, *N. T. Burbidge* 5820, 23.iv.1958 (T.S. 301, 302); "Hillier's Granite", Woodstock, in shelter of overhanging boulders, *N. T. Burbidge* 5957, 30.iv.1958 (T.S. 305) (CANB, PERTH).

Specimens from glass-house plants.—T.S. 298, grown from seed received from *Ealey*, March 1958, harvested 28.x.1958; T.S. 301, 302, grown from seed of *Burbidge* 5820; T.S. 303, grown from seed of *Burbidge* 5873; T.S. 304, grown from seed of *Burbidge* 5910A, granite outcrop between Woodstock Station and Mariana Mill, 28.iv.1958 (no field specimen); T.S. 305, grown from seed of *Burbidge* 5957; T.S. 322, grown from transplants of *Burbidge* 5824, granite outcrop near Gallery Hill, Woodstock Station, 23.iv.1958 (no field specimen).

Long-styled flowers were developed on some plants in the glass-house, usually among those towards the middle section of the raceme. Such flowers proved to be poor seed setters, but the tendency to produce them was not limited to particular plants. The flowers are not strictly vespertine but are very sweet-scented.

The species is an attractive one and might well be used for horticultural purposes. It has leaves similar to those of *N. benthamiana* but cordate, not ovate, in shape, and the upper ones are never sessile. The vestiture is similar in having the ellipsoid-headed glandular hairs with or without specialized stalk cells (see Goodspeed 1954). Such hairs and a similar thinness of leaf texture are also found in *N. cavicola*, described below.

3. **Nicotiana cavicola** sp. nov.

Holotype.—Glass-house plants grown from sample T.S. 202, the original seed collected 7 miles from Meekatharra, Eremaean Province, W.A., in shade of low

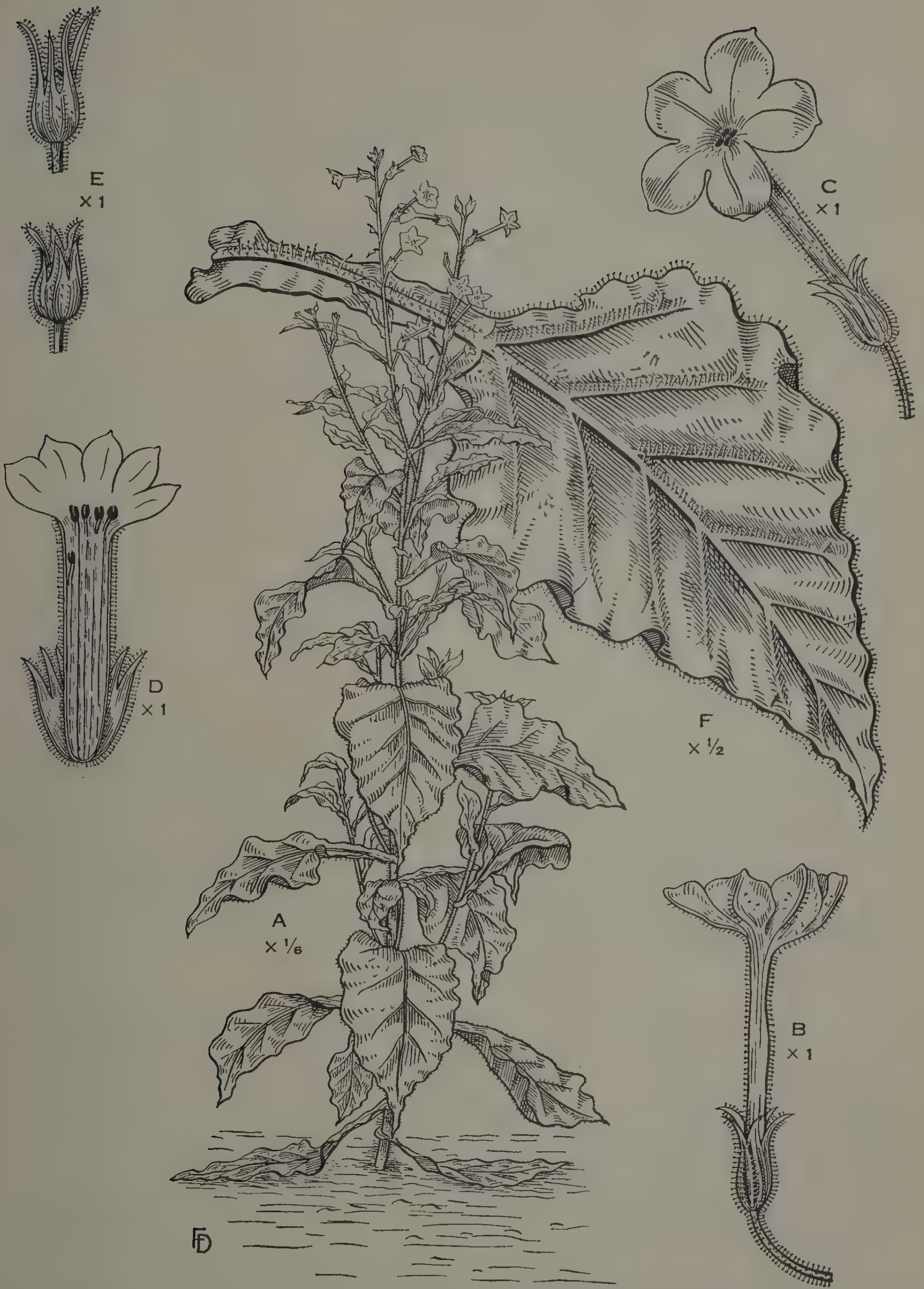

Fig. 7.—*N. cavicola* sp. nov. (drawn from glass-house plant of T.S. 205 = *Burbidge* 4776). Lettering as in Fig. 6. *F*, lower surface of cauline leaf.

outcrop of decomposed granite with a hard lateritic capping, *N. T. Burbidge* 4774, 11.xii.1955 (CANB).

Herba annua foliosa glanduloso-pilosa. *Folia basalia* petiolata, petioli alati, laminae 10–15 cm longae cordatae vel deltoideae acuminatae vel caudatae undulatae, margines irregulariter ciliato-denticulatae; *folia caulina* petiolata laminae deltoideae vel rhomboideae acuminatae; *folia superiora* angusta lanceolata acuminata. *Inflorescentia* paniculata bracteata, bracteae lanceolatae vel lineares. *Calyx* angularis, 9–13 mm longus, nervae prominentes, lobi lineares vel lanceolati obtusi. *Corolla* alba sparse glanduloso-pilosa, tubus 25–45 mm longus, limbus 20–25 mm diametro. *Stamina* inclusa, quattuor adnata, quintum brevius, semiadnatum. *Stigma* breviter exsertum. *Capsula* ovoidea, 8–9 mm longa, calyce persistenti brevior. *Semina* brunnea, testa undulato-reticulata.

Annual leafy herbs, pilose with multicellular hairs with glandular apices (some up to 2 mm long, others short with globular heads). *Leaves* thin in texture, the lower ones to 20 cm long, with broadly cordate or deltoid undulate laminae and winged petioles almost as long and sometimes stem-clasping, the apices of the laminae abruptly narrowed into slender acuminate points or short tails, the margins often minutely but irregularly ciliate-toothed. Stem leaves to 15 cm long, narrower and more or less rhomboid with long acuminate apices but otherwise as in the basal ones; uppermost leaves passing into the leafy bracts of the lower part of the inflorescence. *Inflorescence* paniculate, bracteate, the lower bracts leaf-like, the upper increasingly linear but smaller, pedicels 5–15 mm long. *Calyx* 9–10 mm long, loose around the corolla and with a cupular or urceolate tube which is angular on the short intersepal membranes, the nerves prominent; lobes linear-lanceolate to linear, obtuse but approximately as long as the tube. *Corolla* white, less pilose than the calyx, tube 25–35 mm long (to 45 mm in large-flowered plants), throat 3–4 mm wide (flattened), limb spreading to 20–25 mm diameter, lobes short, broad, and almost truncate-apiculate. *Stamens* enclosed with 4 anthers on short filaments and lying in the throat, the fifth placed lower on a partially adnate filament. *Stigma* in the throat or shortly exserted. *Capsule* 8–11 mm long, ovoid, shorter than the persistent calyx. *Seeds* brown, the surface with a honeycomb pattern of minutely undulate or serpentine reticulated ridges. Chromosome number 23 pairs. (Fig. 7; Plate 11, Fig. 2.)

Except in cases mentioned below, the specimens examined were all obtained from glass-house plants, but they differ little from immature plants seen in the field. The original seed, with one exception, was collected by the author. The species occurs in the area between the Murchison River, Mt. Magnet, Wiluna, and Leonora in the Eremaean Province of Western Australia (Fig. 5). It probably occurs over a wider area of similar country surrounding this part of the State. The plants were invariably associated with "breakaway" hills and outcrops where the undercutting below the hard capping provided shaded sites. Usually the plants were found on the eastern side of the hills or where they were shaded from the midday and afternoon sun. They commonly grew near the sandy hollows where kangaroos and wallabies had made dust baths in the shade. Voucher specimens could not be procured owing to the dry state of the old plants.

In the following list the field numbers and locality data are given after the seed sample number. One field specimen is included.

Specimens Examined.—T.S. 298, Badgeradda Ra., 4 miles S. of Mugga woolshed, Murchison area, Aug.–Nov. 1956, *J. M. Dickens*; T.S. 200, *N. T. Burbidge* 4771, 7 miles E. of Meekatharra, 11.xii.1955; T.S. 201, *N. T. Burbidge* 4773, same locality; T.S. 203, *N. T. Burbidge* 4776, same locality (T.S. 200–205 are all from the type locality and site); T.S. 206, *N. T. Burbidge* 4779, 8 miles E. of Meekatharra, 11.xii.1955; T.S. 207, *N. T. Burbidge* 4780, same locality as 4779; Hillview, 40 miles SE. of Meekatharra, *S. Davies*, Sept. 1959 (field specimen); T.S. 155, *N. T. Burbidge* 4817, between Jones Creek and Kathleen (S. of Wiluna), 13.xii.1955; T.S. 204, *N. T. Burbidge* 4746, Mt. Magnet, on SE. face near rifle range at bases of rock cliffs, 10.xii.1955 (CANB).*

In the Mt. Magnet and Badgeradda Range plants the corollas are larger and longer than in other material. Even larger flowers are present on a specimen (*Gardner* 244A, between Leonora and Laverton, 9.vii.1934—PERTH) which may perhaps belong to *N. cavicola*. The status of this specimen is considered doubtful because the leaves are not entirely typical.

4. **Nicotiana debneyi** Domin in Bibl. Bot., Stuttgart **89**: 593, pl. 36, figs. 6–8 (1929); Goodspeed, Genus *Nicotiana* 483 (1954).

This species has been well described and figured by Goodspeed. It is distinguished from all other Australian species in having the staminal filaments free from the corolla except towards the base of the tube (i.e. "tube proper" of Goodspeed). The seeds are almost straight and the reticulation is of highly serpentine wrinkles (Plate 12, Fig. 1).

It occurs over a wide range of eastern Queensland but does not extend as far west as *N. megalosiphon*. Outside Australia it occurs on Lord Howe Island, and near Noumea in New Caledonia (see Goodspeed, p. 483). It is reported as growing on sandy sites near the sea, but the author has collected it amongst regrowth following fire in disturbed forest near Biloela (inland from Gladstone) and in alluvial soil along a creek north of Injune. (See Fig. 5.)

Specimens grown in Canberra from New Caledonian seed were more robust than is usual in Australian material. The stems were taller and stouter and the corolla tube longer, though the dimensions remained within those quoted by Goodspeed. Possibly there has been some diverging with geographic isolation.

5. **Nicotiana gossei** Domin in Bibl. Bot., Stuttgart **89**: 592, pl. 36, figs. 2–5 (1929); Goodspeed, Genus *Nicotiana* 467 (1954).

A robust foliose species, villous with soft, not viscid, hairs on all parts including the corolla. The large pandurate leaves and the large flowers with their long calyces are characteristic, though a group of specimens from western Queensland

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* In accordance with the author's usual custom all localities in specimen lists are arranged, so far as is possible, from north to south and west to east. The herbarium in which the specimens are housed is indicated after a specimen or series of specimens where consecutive items are in one institution.

A further plant of this species was obtained from a hill on the outskirts of the old mine workings at Cue. It was immature and failed to survive. Other transplant material was obtained on Coodardy Station, west of Mt. Magnet, by S. Davies and E. Slater in September 1959, but it also died.

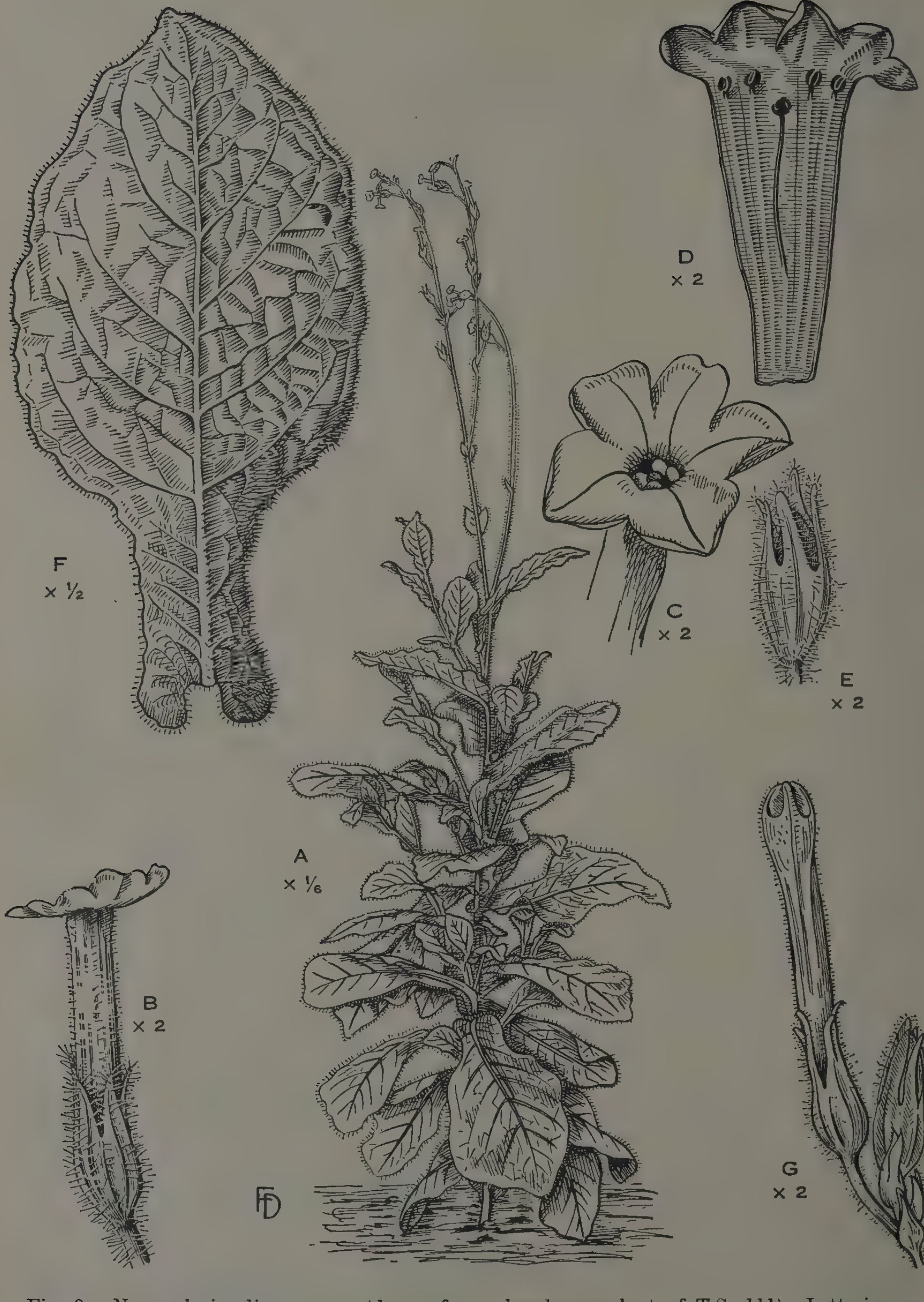
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Fig. 8.—*N. amplexicaulis* sp. nov. (drawn from glass-house plant of T.S. 111). Lettering as in Fig. 7. *G*, buds.

have smaller flowers than those typical of central Australian plants. It is highly probable that these represent plants grown under dry conditions. This opinion is supported by the development of glass-house progeny of undersized field specimens. The seeds are slightly curved and the reticulation is of serpentine wrinkles (Plate 12, Fig. 2).

A figure given in Black's (1957) handbook to the flora of South Australia (2nd Ed., p. 758) as *N. gossei* does not belong to this species. The dimensions of the flowers are too small, the calyx lobes are too short, and the corolla lobes are represented as emarginate instead of obtuse. The drawing may represent a plant of *N. occidentalis*, or a hybrid between *N. gossei* and some other species.

In central Australia the plants of *N. gossei* are found in the rocky gorges of the ranges, such as Palm Valley and Standley Chasm in the MacDonnell Range (see Fig. 5).

6. **Nicotiana amplexicaulis** sp. nov.

Holotype.—Carnarvon Ra., 63 miles S. of Rolleston, Qld., at base of sandstone cliff and in lee of overhanging rocks, *N. T. Burbidge* 5562, 13.ix.1956 (CANB).

Herba annua, pubescens. *Folia* sessilia basi auriculata amplexicaulia; folia basalia ovalia vel oblonga, ad 30 cm longa et 20 cm lata, margines sinuata; folia caulina pandurata vel spathulata, 10–20 cm longa, obtusa vel acuta, margines integra vel sinuata; folia superiora oblonga vel obovata. *Inflorescentia* paniculato-ramosa, rami pubescentes, pedicelli bracteati, bracteae ovatae vel lanceolatae acuminatae. *Calyx* 8–12 mm longus, lobi lanceolati acuminati pubescentes, pili simplices glandulosi. *Corolla* alba pubescens, tubus 15–18 mm longus, limbus 10–14 mm diametro. *Stamina* inclusa, quattuor adnata, quintum brevius et supra basim liberum. *Capsula* ovoidea vel ellipsoidea, 6–8 mm longa, calyce persistenti brevior. *Semina* brunnea, rugis undulatis.

Herbs with a simple erect leafy stem or branched from near the base, the branches and other parts pubescent with multicellular hairs. *Leaves* in the lower two-thirds of the plants, thin in texture, pubescent on the principal nerves especially on the lower surface, glabrescent between, sessile but with conspicuous stem-clasping rounded auricles, apices acute or obtuse, margins entire or slightly sinuate in the lower leaves. Lower leaves comparatively large, oval or oblong, and to 30 cm or more in length; the principal stem leaves pandurate, being broad above and slightly or much narrowed below before broadening into the auricles, 10–15 cm long; uppermost leaves shorter and oblong to obovate. *Inflorescence* paniculate, the lowest branches arising from the upper leaf axils; pedicels bracteate, 5–15 mm long; bracts long with narrow lanceolate acuminate lobes slightly longer than the tube, the intersepal membranes not conspicuous, pubescent with long multicellular hairs mixed with shorter capitate glandular ones (simple type). *Corolla* white, pubescent, with multicellular hairs shorter than those of the calyx, tube 15–18 mm long, very narrow in the lower 4–5 mm, the throat 3–4 mm wide (flattened), limb spreading but deflexed on the upper side in fresh plants, 10–14 mm in diameter, with very shallow rounded but emarginate lobes. *Stamens* enclosed, 4 adnate except for a very short length below the anthers which lie in the throat, the fifth shorter and with a filament free except in the narrow part at the base of the tube, anthers 1·25 mm long. *Stigma* barely exserted. *Capsule* ovoid or ellipsoid, 6–8 mm long, slightly shorter than the persistent calyx. *Seeds* brown, deeply undulate wrinkled. Chromosome number 18 pairs. (Fig. 8; Plate 13, Fig. 1.)

Specimens Examined.—Carnarvon Ra., 52 miles S. of Rolleston, Qld., under lee of rocks in cliff, *N. T. Burbidge* 5560, 13.ix.1956; glass-house plants of T.S. 111 grown from seed collected at Moolayember, Carnarvon Ra., via Injune, Qld., *M. S. Stevens*, received Canberra 18.x.1954 (CANB); Moolayember region, *M. S. Stevens*, December 1954 (CANB, BRI).

Burbidge 5560 and 5562 (holotype) are also represented by transplants which were matured in the glass-house under T.S. 286.

The new species appears to be limited to the Carnarvon Range, on the boundary of the Leichhardt and Maranoa districts in Queensland (see Fig. 5). It grows in shaded habitats below overhanging cliffs. The flowers are not markedly vespertine. It approaches *N. debneyi* (with 24 pairs of chromosomes) but it differs in being softly pubescent and in lacking the ellipsoid-headed glandular hairs. The stem-clasping auricles are larger in proportion to the laminae than in *N. debneyi*, the flowers are larger and have a broader tube and limb. The stamens differ in not being all inserted low in the tube. The vestiture gives the plants a resemblance to *N. gossei* but in the latter species the plants are much more robust and the flowers much larger. There is little difference between field and glass-house plants.

7. **Nicotiana maritima** Wheeler in Univ. Calif. Publ. Bot. **18**: 56 (1935); Goodspeed, Genus *Nicotiana* 463 (1954).

The flowers of this species resemble those of *N. velutina*, but the plants are more robust with erect, sometimes simple stems, and the vestiture is more or less villous, with the hairs often reflexed and appressed instead of minutely puberulent as in the inland *N. velutina*. As indicated in the key, the seeds of the two species are quite different in appearance (Plate 13, Fig. 2; Plate 14, Fig. 1).

N. maritima is mainly found in coastal areas and is known from the coasts of the Australian Bight to those of Victoria (see Fig. 1).

8. **Nicotiana velutina** Wheeler in Univ. Calif. Publ. Bot. **18**: 55 (1935); Goodspeed, Genus *Nicotiana* 465 (1954).

A common and widespread species occurring in central Australia, western and south-western Queensland, South Australia, and western New South Wales (see Fig. 1). It does not seem to have spread far into Western Australia, though one would expect to find it along the eastern boundary. It grows in sandbanks left by floods along the inland river courses and on sandhills. Apart from the puberulent vestiture, it may be recognized by the comparatively broad corolla tube and narrow limb and by the curved-reniform seeds (Plate 14, Fig. 1).

Small-flowered specimens of this species have been mistaken for *N. rotundifolia*, which is a species of southern and south-western Western Australia. So far as is known, these two species do not occur in the same area unless their distribution overlaps in the vicinity of the Nullarbor Plain.

9. **Nicotiana hesperis** sp. nov.

Holotype.—Rocky Pool, Gascoyne R., E. of Carnarvon, N.T., *Burbidge* 6494A, 3.ix.1959 (CANB).

Affinis *N. occidentali* sed hirsuta et gracilis, calyx angustior, corolla brevior, capsula ellipsoidea.

Herba annua erecta hirsuta, pili viscidi glandulosi. *Folia radicalia* obovata vel lanceolata vel spathulata obtusa, ad basim angustiora vel breviter petiolata. *Folia caulina* sessilia oblonga vel elliptica, superiora linearia minora. *Inflorescentia* simplex vel ramosissima bracteata, bracteae minutae lineares, flores pedicellati frequenter cleistogami. *Calyx* gracilis 8–11 mm longus 2–3 mm diametro, lobi gracilis lineares subaequales vel inaequales, in floribus tubo subaequales, membranae conspicuae. *Corolla* alba vel extus pallido-virescens, tubus in floribus chasmogamibus 12–25 mm longus 1–3 mm diametro, limbus 4–6 mm latus breviter lobatus, lobi emarginati, fauces symmetros, tubus in floribus cleistogamibus brevior. *Stamina* quattuor in faucibus, dua filamentibus longioribus; quintum brevius filamenta semiadnata. *Capsula* gracilis ellipsoidea 6–10 mm longa 2·5–4·5 mm diametro. *Semina* curvatissima dorsaliter plana vel cristata, testa reticulata, reticulo semitransversi.

Hirsute herbs with a cluster of radical leaves and smaller cauline ones. Stems, pedicels, and calyces hirsute with conspicuous spreading multicellular hairs with ellipsoid glandular apices. *Basal leaves* obovate, oblanceolate, or spathulate, obtuse, narrowed below into a short slender petiole. *Cauline leaves* sessile oblong or elliptical, the uppermost linear and passing into the minute bracts of the inflorescence. *Inflorescence* forming the major part of the plant, main shoot usually bearing its first flower among the basal leaves and with several flowering shoots arising from the lower axils, sometimes simply subracemose but much branched in larger plants. *Flowers* pedicellate, often cleistogamous. *Calyx* slender, 8–11 mm long and less than 3 mm in diameter, lobes slender, subequal or unequal, the longest about as long as the tube in the flower but proportionately shorter in the mature capsule, the intersepal membranes conspicuous and extending almost to the base. *Corolla* highly variable in size from slightly longer than the calyx in cleistogamous flowers to about 2½ times as long in normal ones, tube 1–3 mm diameter at top of calyx but slightly wider above, swollen about the upper anthers; limb 4–6 mm wide with shallow emarginate lobes, white within but often pale greenish without. *Stamens* with 4 in the throat arranged in pairs of which 1 has slightly longer filaments, the fifth lower in the tube and on a filament free above the base of the tube and lying between the longer of the upper pairs. *Capsule* slender, ellipsoid, 6–10 mm long, 2·5–4·5 mm diameter. *Seeds* strongly curved with the ends pressed together leaving a deep furrow on either side, the reticulation slightly serpentine but the ridges subparallel and more or less transverse, the dorsal surface either broader and flattened at right angles to the sinus or pressed out in a thin but conspicuous crest. Chromosome number unknown (Fig. 9; Plate 15).

This species is distinguishable from *N. occidentalis* subsp. *occidentalis* by the more hirsute vestiture, the smaller stature with the inflorescence forming most of the plant, the marked tendency to produce basal flowers, the more frequent

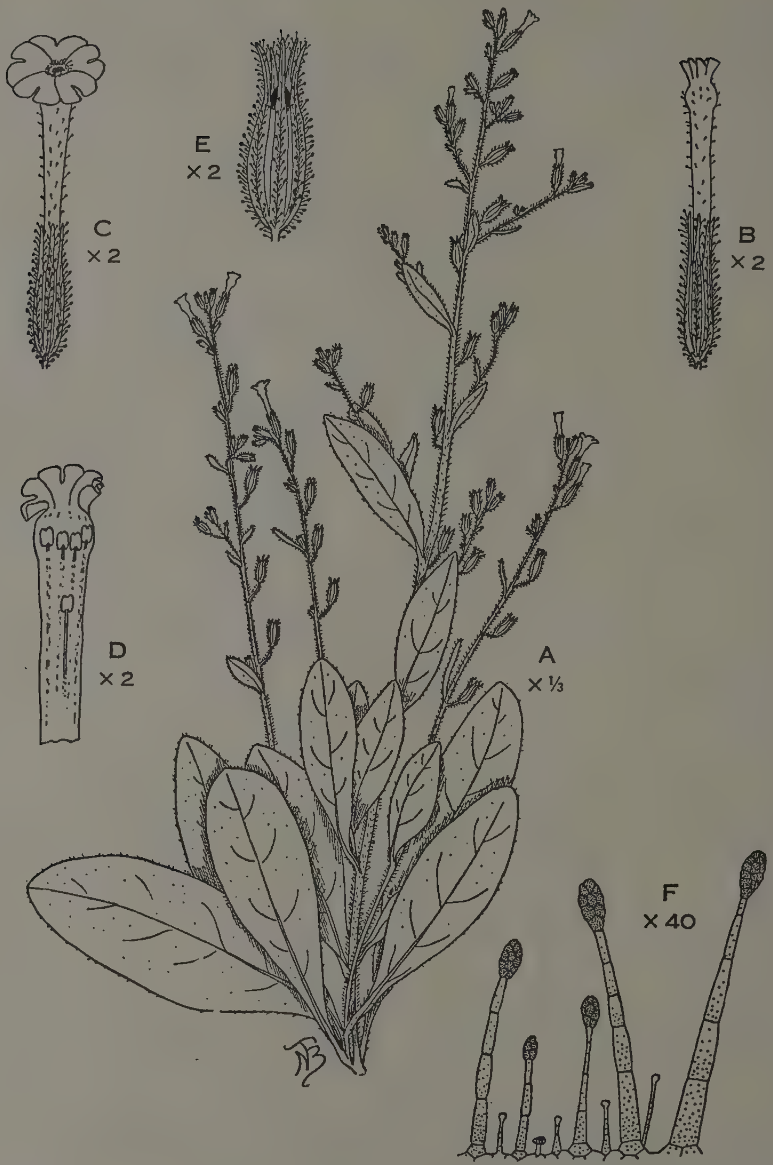


Fig. 9.—*N. hesperis* sp. nov. (drawn from *Burbidge* 6494). Lettering as in Fig. 6. *F*, trichomes from pedicel, showing ellipsoid-headed glandular hairs, small simple or immature ones, and a single hydathode.

cleistogamy, the narrow calyx and capsule, and the broader symmetrical corolla tube. The most striking character is that of the seeds, with their peculiar U-shape and transverse markings which give a "concertina" appearance. The presence or absence of a crest on the back of the seed is not related to other morphological differences and appears to vary within populations.

In a number of specimens the corolla limbs are eaten by small caterpillars and the corolla then has a truncate appearance.

Plants belonging to *N. hesperis* include at least one of those quoted as possible variants of *N. occidentalis* by Wheeler under her original description. This is the case with a specimen from near Roebourne, collected by Carey (MEL). Two other Melbourne sheets, "Yuin 1888, Hy . . ." and "between Northampton and Shark Bay, Carey 1844", have larger flowers with well-developed corolla limbs and seeds as in *N. occidentalis*. The flowers on these specimens are unusually showy for *N. occidentalis*, but are best placed with it.

N. hesperis occurs in the coastal and subcoastal areas of Western Australia, between Roebourne in the north and Dongarra in the south (Fig. 4). Because it is the most western of the Australian species it has been named accordingly. It was found to be common between Northampton and Carnarvon during a field trip made in September 1959. Its eastern limit is not known but may be less than a hundred miles inland. Its distribution overlaps that of *N. occidentalis*.

Specimens Examined.—Roebourne, *Carey* 1884 (MEL); N. of Wooramel R. bridge, *N. T. Burbidge* 6485, 2.ix.1959; Wooramel R. bridge, *N. T. Burbidge* 6480, 2.ix.1959: between Woodleigh Station and Wooramel R., *N. T. Burbidge* 6473, 2.ix.1959; near Woodleigh homestead, *N. T. Burbidge* 6451, 2.ix.1959; 1 mile E. of Woodleigh homestead, *N. T. Burbidge* 6461, 2.ix.1959; S. of Hamelin Pool turn-off, *N. T. Burbidge* 6507, 4.ix.1959; 46 miles N. of Murchison R. bridge, *N. T. Burbidge* 6445, 1.ix.1959; 19 miles N. of Murchison R. bridge, *N. T. Burbidge* 6443, 1.ix.1959; between Greenough and Dongarra, *N. T. Burbidge* 6519, 5.ix.1959 (CANB).

10. **Nicotiana occidentalis** subsp. **occidentalis**

N. occidentalis Wheeler in Univ. Calif. Publ. Bot. **18**: 52 (1935); Goodspeed, Genus *Nicotiana* 479 (1954) (pro parte).

The type of Wheeler's species is a specimen "Port Hedland, 11 Aug. 1911, *Mjoberg* 105" held by the National Herbarium of New South Wales in Sydney. Examination of this shows that the corolla tube is relatively slender and without the oblique limb found in specimens from the more inland areas. As a consequence the flowers have a greater resemblance to those of *N. megalosiphon* (see Plate 8, Fig. 1), but the plants can be distinguished by the presence of the characteristic ellipsoid-headed glandular hairs, by the subdidynamy of the upper stamens, and by the curved (C-shaped) seed with wrinkled reticulation. A specimen illustrating this corolla form is to be seen on the right hand of the Kew sheet showing Clement's specimen of *N. benthamiana* (Plate 2). Other matching specimens include one collected near Port Hedland by Cleland (AD95929135) and one from Trimoville, Monte Bello Islands, *Hill*, 10.xi.1953 (CANB). For the general distribution see Figure 4.

During a field trip in May 1958, transplant material of *N. simulans* (see below) was obtained between Meekatharra and Nannine. In accordance with the usual practice the original soil was tested for residual seed, with the result that plants of *N. occidentalis* subsp. *occidentalis* were obtained, but they were atypical in that the stems were unusually slender and all flowers were cleistogamous. Second generation plants were similar, but those placed in a cooler glass-house produced thicker stems and developed more normal flowers. These plants (T.S. 321) show that the subspecies extends well inland and to the south of the Pilbara, but being atypical they do not form a satisfactory base for discussing the relationships between it and the subspecies described below.

Among the specimens quoted by Wheeler is one collected at Greenough by Helms, and a duplicate of this, held at Sydney, has been examined. The size of the flower is larger than that found in *N. hesperis* from the same area, though on geographic grounds it might be anticipated that it would prove to be the same. Unfortunately the seeds on this specimen are too immature for diagnostic purposes. For the present it must be assumed that this specimen and the large-flowered specimens "Yuin, Hy. . ." and "between Northampton and Shark Bay, Carey" (both MEL), represent subsp. *occidentalis* in a southern form.

11. **Nicotiana occidentalis** subsp. **obliqua** subsp. nov.

N. occidentalis Wheeler, Univ. Calif. Bot. Publ. **18**: 52 (1935) (pro parte); Goodspeed, Genus *Nicotiana* 479 (1954) (pro parte).

Holotype.—Victorian Desert, Camp 53, *Helms*, 15.ix.1891 (NSW).

Corolla zygomorpha, limbus in floribus juvenalibus obliquus, stamina superiora subdidynama.

In this subspecies, of which many samples have been grown in the glass-house, there are marked differences between field specimens and glass-house plants. In field material the plants may be less than 40 cm high with one or few stems from the base, the basal leaves are not persistent, and the stem leaves are sessile, or if narrowed below then more or less auriculate or pandurate. The vestiture on all parts of the plants consists of ellipsoid-headed glandular hairs whose sticky secretion is responsible for the adherence of soil and vegetable fragments. The inflorescence commonly forms more than half of the plant. The corolla tube may be less than 20 mm long (up to 35 mm in the holotype and in a specimen from between the Musgrave and Everard Ranges, *J. B. Cleland*, 28.ix.1945 (AD95631035)) but the upper stamens are subdidynamous, and the throat longer on the upper side so that the limb is distinctly oblique, especially in well-formed buds and (less characteristically) in withered flowers. (Plate 8, Fig. 2.)

In glass-house plants the stems are robust and may be up to 1 metre high. In the basal rosette the leaves are obtusely spathulate with long strap-like bases. The cauline leaves are at first similar, but pass into a pandurate shape and then become more or less linear-lanceolate. It is this type of plant that is figured by Goodspeed (1954, Fig. 114). The inflorescence in such individuals rarely involves more than a third of the height of the plant; the bracts vary from linear, as illustrated by Goodspeed, to the broader, often ovate shape indicated in a text figure on p. 757 of Black's (1957) handbook to the flora of South Australia (2nd Ed.). It must be assumed that under good habitat and seasonal conditions field plants similar to those cultivated would be collected.

Since the seed character (Plate 14, Fig. 2) remains constant in the two subspecies, the chief difference between them is the asymmetry of the corolla. This character was employed in the key provided by Goodspeed for a number of species, but in the author's experience it is only in this case and in *N. simulans* that it is sufficiently evident in dried material to be a good diagnostic feature. In other species placed by Goodspeed in the same group, such as *N. debneyi*, *N. exigua*, and *N. rotundifolia*, the throat is not longer on one side but the limb is reflexed on the upper side—quite a different condition from that seen in *N. occidentalis* subsp. *obliqua* and *N. simulans*.

The latter type of modification of the corolla arises from the unequal elongation of the throat, which results in a lifting of one pair of upper stamens and in the bending of the whole limb into an oblique position. The character is best seen in well-developed buds, as very young buds are straight and open flowers are rarely pressed from the best angle to demonstrate the condition. Withered flowers may also have an oblique limb, but such shapes may also be seen in specimens of other species. (Plate 8, Fig. 2.)

The inland form of *N. occidentalis* is very widespread. It is represented by specimens from as far apart as the Ashburton and Murchison Rivers in Western Australia (see Wheeler 1935) and western Queensland (Headingly Station, *Everist* 3318, 2.xii.1947—BRI, CANB) and in South Australia as far south as the Gawler Range, west of Port Augusta (plants grown as T.S. 198). (See Fig. 4.)

Selection from Specimens Examined

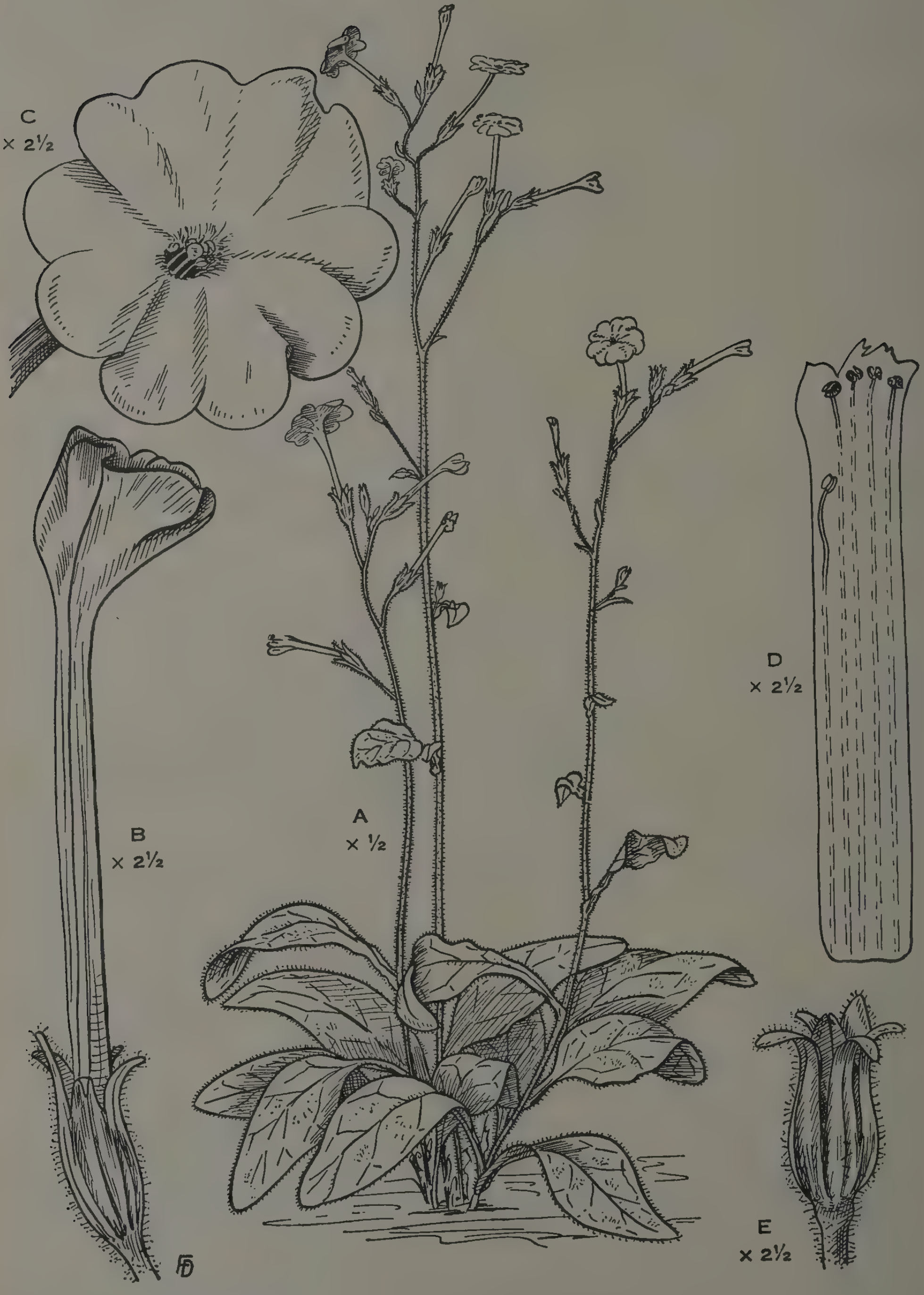
WESTERN AUSTRALIA: Cane and Ashburton Rivers, *A. Forrest* 1878; Fortescue R., *H. S. Carey* 1878 (MEL); Wooleen, E. of Errabiddy Hills, *J. M. Dickens*, Aug.–Nov. 1956 (seed only—grown as T.S. 290) (CANB); ex Univ. Calif. No. 40-32, strain originally from Yalgoo, collected *Pierce* (NSW); 1½ miles N. of Leonora, *N. T. Burbidge* 4844, 14.xii.1955 (seed only—T.S. 176); 6 miles E. of Murrin, *N. T. Burbidge* 4850, 15.xii.1955 (seed only—T.S. 181); 17 miles W. of Laverton, *N. T. Burbidge* 4853, 15.xii.1955 (voucher for T.S. 182); Goddard Creek, N. of Zanthus, without collector's name, grown as T.S. 236 (CANB). CENTRAL AUSTRALIA: 5 miles W. of Mt. Riddoch, *N. T. Burbidge and M. Gray* 4495, 1.x.1955 (original specimen mixed with *N. simulans*) (CANB); slopes of Mt. Gillen, *J. B. Cleland*, 9.viii.1936 (AD); Charlotte Waters, *G. Chippendale* 1332, 6.vii.1955 (NSW); Ernabella, Musgrave Ra., *J. B. Cleland*, 24.viii.1954; between Musgrave and Everard Ra., *J. B. Cleland*, 28.ix.1945; Gawler Ra., between Yardea and Nonning, *J. B. Cleland*, Oct. 1954 (AD). QUEENSLAND: Headingly Station, Gregory North, *S. L. Everist* 3318, 2.xii.1947 (BRI, CANB).

12. **Nicotiana simulans** sp. nov.

Holotype.—Between Mt. Willoughby and Mabel Creek, S.A., *N. T. Burbidge and M. Gray* 4625, 10.x.1955 (CANB) (voucher for glass-house plants under T.S. 163).

Affinis *N. occidentali* sed folia et semina ut in *N. megalosiphone*.

Herba annua glandulosi-pubescens. *Folia radicalia* laminae ovatae vel spathulatae vel lanceolatae, ad basim attenuata, apices obtusae; *folia caulina* similans sed laminae lanceolatae vel ellipticae obtusae vel acuminatae. *Inflorescentia* racemosa vel paniculata, bracteae parvae. *Calyx* 9–13 mm longus, tubus gracilis, membranae conspicuae, lobi subaequales subteretes divaricati vel recurvi. *Corolla* minute pubescens alba, tubus gracilis 30–40 mm longus 1·5–2·5 mm diametro, lobi emarginati, limbus obliquus. *Stamina* quattuor subdidynama in faucibus, quintum brevius filamenta semiadnatam. *Capsula* lato-ellipsoidea vel ovoidea 9–11 mm longa, calyce persistenti brevior. *Semina* brunnea reticulata, reticulum alveolatum.


C
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E
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Fig. 10.—*N. simulans* sp. nov. (drawn from glass-house plant of T.S. 311 = *Burbidge* 6077). Lettering as in Fig. 6.

Annual herbs, the pubescence with hairs of varying length and including glandular hairs terminating in single globular cells. *Leaves* mainly radical in field specimens, but with elliptical or lanceolate cauline leaves narrowed below, sometimes narrowly auriculate, rarely slightly decurrent, apices obtuse to acuminate. *Inflorescence* often subracemose in field specimens but paniculate in large plants, the branches with minute linear bracts. Pedicels 10–20 mm long, the lower ones with bracts and evidently representing reduced branches. *Calyx* 9–13 mm long, lobes linear or conduplicate-terete, spreading or recurved and subequal, at anthesis as long as or longer than the tube, intersepal membranes conspicuous and extending almost to the base, the nerves prominent. *Corolla* white and minutely pubescent outside, tube slender, 30–40 mm long, 1·5–2·5 mm in diameter (when flattened), throat longer on the upper side so that the limb is slightly oblique, limb to 20 mm in diameter, lobes rounded emarginate. *Stamens* with the upper 4 stamens subdidynamous and on unequal filaments, fifth with a longer filament but placed lower in tube. *Style* with the stigma shortly exserted or placed a little above the upper anthers. *Capsule* ellipsoid or ovoid, 9–11 mm long and about two-thirds as long as the persistent calyx. *Seeds* slightly curved but angular towards the broader end, reticulation in honeycomb pattern with the junctions of the sharply raised ridges forming short points so that the seeds are rough in silhouette. Chromosome number 20 pairs. (Fig. 10; Plate 16, Fig. 1.)

N. simulans lies between *N. occidentalis* and *N. megalosiphon*. It has a corolla similar to that of *N. occidentalis* subsp. *obliqua*, with which it may be associated in the field, but it differs in the elliptical cauline leaves, in the lack of the sticky ellipsoid-headed glandular hairs, and in the honeycomb pattern of the testa. It also differs in the chromosome number. It may be distinguished from *N. megalosiphon*, whose habit may be similar, by the size and shape of the corolla. In *N. megalosiphon* the longer corolla tube is not asymmetrically flared at the throat, which is slightly swollen around the subsessile upper anthers. Above these in the bud the limb is slightly constricted and then neatly flared in the conduplicate lobes. The appearance of fresh buds of *N. simulans*, *N. megalosiphon*, and *N. occidentalis* subsp. *obliqua* is shown in Plates 8 and 9. In *N. megalosiphon* and *N. simulans* the testa pattern is of the honeycomb type, but in the new species it is coarser in texture (Plate 16).

In a specimen from Erong-Dalgetty Downs, Gascoyne, W.A., *S. Davies*, 24.ix.1959, the buds are atypical in being shaped like those in *N. megalosiphon*. Examination of the stamens shows that the upper anthers are not subsessile and at the same level as in the eastern species, but are on slightly unequal though short filaments, and the lower anther is much lower in the tube than is the case in *N. megalosiphon*. In other respects—habit, size of flowers, and seeds—the specimen agrees with other material of *N. simulans*. It must be suspected that this bears a relationship to *N. simulans* similar to that between the subspecies of *N. occidentalis*. Only further collectings will show whether this form is important.

It will be evident from the above remarks that *N. simulans* may be distinguished, not by peculiar characters, but by the combination of characters otherwise found in differing species.

In some glass-house plants the flowers tend to become cleistogamous, and in this condition a worker unfamiliar with the species might confuse it with *N. rotundifolia*, though this latter species can be separated on the seed character. Cleistogamy is closely related to day length, as was shown by a test carried out by Dr. L. Evans of the Division of Plant Industry, C.S.I.R.O., on plants grown from seed of transplants collected between Meekatharra and Nannine in Western Australia. Under long day conditions the flowers were chasmogamous with normal corollas, though on some plants the basal flower of an inflorescence had a short corolla which failed to open. Under a short day regime flowering was markedly delayed, and about 8–12 of the flowers along a branch were cleistogamous with undersized corollas, though occasionally the apical flower was normal and chasmogamous.

A large number of specimens of *N. simulans* have been examined, many being glass-house plants from seed collected by the author in central Western Australia and in central Australia. Specimens from the herbaria at Sydney, Melbourne, Adelaide, and Perth have also been studied, and may be inspected at the relevant institutions. The list provided below is a selection to indicate the geographic distribution.

The new species is widely distributed in the arid areas of central Australia. It is common in the mulga country of the Eremaean Province of Western Australia, is found in central and South Australia, and extends eastward to western New South Wales (see Fig. 3). It is usually found amongst the ephemeral growth in the shade of *Acacia* bushes and trees, or in the litter near fallen branches. It is frequently found near minor water channels but rarely associated with major creeks and rivers.

Selection from Specimens Examined

WESTERN AUSTRALIA: 41 miles S. of Roy Hill, *N. T. Burbidge* 6031, 8.v.1958 (also glass-house plants T.S. 306) (CANB); Minilya R., N. of Shark Bay, *J. Forrest* (MEL); Lyons R., *S. Davies*, 21.ix.1959; Dalgetty Downs, *S. Davies*, 24.ix.1959; Erong-Dalgetty Downs boundary, *S. Davies*, 24.ix.1959; (atypical plants) (CANB); upper Murchison R., *Isaac Tyson* (MEL); 108 miles S. of Mundiwindi, *N. T. Burbidge* 6082, 9.v.1958 (voucher for seed T.S. 314); 23 miles E. of Meekatharra, *N. T. Burbidge* 4785, 11.xii.1955 (seed only = glass-house plants of T.S. 210); 40 miles S. of Lawlers, N. of Doyle's Well, *N. T. Burbidge* 4822, 14.xii.1955 (seed only = glass-house plants of T.S. 170); 1½ miles N. of Leonora, *N. T. Burbidge* 4845, 14.xii.1955 (seed only = glass-house plants of T.S. 177); 15 miles W. of Laverton, *N. T. Burbidge* 4856, 15.xii.1955 (seed only = glass-house plants of T.S. 183); 14 miles S. of Melita turn-off on Leonora–Menzies road, *N. T. Burbidge* 4867, 16.xii.1955 (seed only = glass-house plants of T.S. 188); 5 miles of Menzies, *N. T. Burbidge* 4871, 16.xii.1955 (CANB); Victoria Desert, Camp 53, *Helms*, 15.ix.1891 (NSW). CENTRAL AUSTRALIA: Haast's Bluff, *J. B. Cleland* 38a, 70a, Aug. 1956 (AD); 2 miles W. of New Huckitta homestead, *M. Lazarides* 5963, 11.ix.1955 (mixed with *N. occidentalis*); between Alice Springs and Undoolya, *N. T. Burbidge and M. Gray* 4177, 19.ix.1955 (voucher for glass-house plants of T.S. 238) (CANB); Alice Springs, *G. Chippendale* 3057, 15.ix.1956 (CANB, NSW); 5 miles N. of Mt. Cavenagh Station, *R. A. Perry* 5507 (voucher for glass-house plants of T.S. 134) (CANB). SOUTH AUSTRALIA: Ernabella, *J. B. Cleland*, 25.ix.1944 and 25.ix.1945 (AD); N. Musgrave Range, *Basedow* 258, July 1926 (NSW); Charlotte Waters, *Giles* (MEL); Mt. Chandler Well, 200 miles W. of Oodnadatta, *J. B. Cleland* 29.ix.1945 (AD); 1 mile W. of Oodnadatta, *R. A. Perry* 5550, 13.ix.1955 (voucher for glass-house plants of T.S. 138) (CANB); Mt. Lyndhurst, *Koch*, 1897 (NSW). NEW SOUTH WALES: Darling R., *Mrs. B. Kennedy* 1886 (MEL); Barrier Ra., *Mrs. Irvine* 1889 (MEL); near Corella tank, Bourke, *E. N. McKie*, 19.iv.1939 (NSW).

13. **Nicotiana megalosiphon** Heurck & Muell. Arg. in Van Heurck, Obs. Bot. 126 (1870) (non vidi); Goodspeed, Genus *Nicotiana* 471 (1954).

The most "typical" specimens of this species are those from the open forests of eastern and south-eastern Queensland. To these, with their very long and slender corolla tubes, the specific epithet is particularly applicable. Further inland, long-tubed flowers (up to 90 mm long) may be found, but there is a tendency for shorter ones (down to 40 mm long). In dry habitats in south-western Queensland the plants may have few cauline leaves above the more persistent basal rosette.

The species is close to *N. simulans* (see above) but may be distinguished by the longer corolla tube, by the sessile or subsessile upper anthers which are never subdidynamous, by the shortly filamented lower stamen which is placed only slightly below the upper group, by the symmetrical throat, and by the shape of the buds (Plate 8, Fig. 1). The testa pattern is finer than in *N. simulans* (Plate 16, Figs. 1, 2).

N. megalosiphon extends to central Australia, having been collected by the author in the vicinity of Alice Springs (*Burbidge* 4203, 4236, 4371), where the fragrance of the vespertine flowers helped to distinguish it from *N. simulans*. It has not been found in Western Australia, but an atypical plant of *N. simulans* which resembled it has been discussed under the latter species.

Wheeler (1935) quoted three Western Australian specimens in her remarks (but not in her specimen list) under *N. megalosiphon*. These specimens are held at Melbourne. In the author's opinion, Forrest's specimen from Minilya represents *N. simulans*, while Forrest's Gascoyne River specimen and that from the Wooramel River collected by Robinson are both better placed with *N. rosulata*, though as the last-named consists of flowers only the determination is not completely certain.

14. **N. rotundifolia** subsp. **rotundifolia**

N. rotundifolia Lindley, Bot. Reg. **24**: misc. 59 (1838); Wheeler in Univ. Calif. Publ. Bot. **18**: 62 (1935) (pro parte); Goodspeed, Genus *Nicotiana* 481 (1954) (pro parte); *N. fastigiata* Nees in Lehmann, Pl. Preiss. **1**: 343 (1844); *N. neesii* Lehmann ex Nees in Lehmann, Pl. Preiss. **1**: 344 (1844).

Erect plants with leafy villous stems less than 10 cm high in small plants but up to 100 cm high and 1 cm diameter at base in large plants. Inflorescence forming less than half the height (Plate 5, Fig. 1). Calyx lobes lanceolate and acuminate, flat or the margins slightly incurved towards the apices, intersepal membranes usually inconspicuous or evident at the top of the tube (Plate 7). Seeds slightly curved, with a well-raised honeycomb pattern in which the ridges are slightly undulate-serpentine (Plate 17, Fig. 1).

Among large specimens examined were some from Northam, W.A., which were 50–80 cm high in the field (*Burbidge* 4988, 4989, 4990—11.i.1956), and in the glasshouse produced progeny of more than 100 cm (T.S. 195, 196, and 169—corresponding to the field numbers above). The smallest plants were collected in the lee of a large boulder on Badjanning Hill, near Wagin, W.A. (*Burbidge*, sine no., Dec. 1955). These were under 10 cm high, but retained the leafy stems and produced progeny of intermediate size (T.S. 294).

Examination of material placed with *N. rotundifolia* has revealed that there are two forms, the one discussed above being found in the South West Province and the other (see below) in the drier areas of the Province and in the areas to the east. Lindley's description best fits the western form, and it is unlikely that the inland form would have been sent to him at such an early date. In both forms the chromosomes number 22 pairs.

Of the two synonyms, *N. fastigiata* Nees is superfluous, having been given to *N. rotundifolia* on the basis of the unsuitability of Lindley's name, the leaves being rarely if ever truly rotund. Nees quoted a specimen, *Preiss* 1911, under his *N. fastigiata*, and a duplicate of this, held at Melbourne, has been examined and found to agree with other specimens of *N. rotundifolia* subsp. *rotundifolia*.

N. neesii Lehmann is described as having reflexed flowers and fruits, but with a plant form which agrees with subsp. *rotundifolia*. Among the progeny of T.S. 196 (*Burbidge* 4989) were some which failed to produce the stout erect stem and developed numerous short slender basal shoots of the "secondary" type (Plate 6, Fig. 1). On such plants the flowers were variable in size and slightly smaller than in robust plants, but the pedicels were longer (up to two or three times the length of the calyx). The pedicels were commonly down-curved during flowering but erect in the capsule stage (Plate 7, Figs. 1, 2). Since Lehmann describes the flowers as being "longe pedunculatis", there is a possibility that his name was based on a plant of this type. A similar variation is found in the field specimens, where some of the material has long-pedicelled flowers and capsules which are divaricately spreading from the stem, though in robust specimens the pedicels are short and erect. In some specimens the calyx lobes have incurved margins, and this state may correspond to that described by Lehmann "laciniis calycis lineari-subulatis", which otherwise applies better to the subspecies described below.

In all specimens examined the corolla lobes are rounded and emarginate as described by Lindley. Corolla lobes agreeing with "rotundatis obtusis" (*N. fastigiata*) or with "acutis" (*N. neesii*) have not been observed.

The name *N. rotundifolia* has been applied to plants from various parts of arid Australia, but no authentic material from localities other than those in Western Australia has been seen. Its occurrence in the mulga areas of the Eremaean Province of Western Australia is doubtful, though the subspecies described below occurs in the southern areas with an average rainfall of more than 10 inches per annum and a vegetation dominated by *Eucalyptus* spp., or by *Acacia* spp. other than *A. aneura* F. Muell. It is unlikely that the species extends to central Australia, though it possibly reaches the western parts of South Australia. (See Fig. 5.)

Other Specimens Examined.—Mogumber, *W. V. Fitzgerald*, Nov. 1903, det. Wheeler (NSW); eastern sources of Swan R., *Mrs. Heal*, 1889; between Swan R. and King George's Sound, *J. Forrest*, 1881; sources of Blackwood R., *Miss Cronin*, 1893 (MEL).

15. **Nicotiana rotundifolia** subsp. **aridicola** subsp. nov.

N. rotundifolia Lindley sensu Wheeler, Univ. Calif. Publ. Bot. **18**: 62 (1935) (pro parte); Goodspeed, Genus *Nicotiana* 481 (1954) (pro parte).

Holotype.—Pioneer Rock, N. of Lake Cowan, W.A., *N. T. Burbidge* 2668, 19.ix.1947 (CANB).

Folia omnia radicalia nonnunquam folia caulina pauca. Tubus calycis gracilis, membranae conspicuae, lobi lineares vel linearo-subulati. Reticulum testae undulatum.

In this subspecies the plants have a well-developed cluster of radical leaves and a group of erect, almost leafless flowering stems more than half the height of which forms the inflorescence (Plate 5, Fig. 2). Cauline leaves are developed on some glass-house plants but only in the lower part of the stems. The leaves are obtuse and commonly dry off before seed setting is completed. The stems are villous below and may be glabrescent above except on the pedicels and calyces. The calyx is slender, cylindrical or ellipsoid, with conspicuous intersepal membranes extending almost to the base and with narrow linear or linear-subulate lobes. The seeds resemble those of subsp. *rotundifolia* but the ridges are more definitely serpentine and not as sharply raised. (Plate 5, Fig. 2; Plate 6, Fig. 2; Plate 17, Fig. 2.)

The recognition of two forms under *N. rotundifolia* has been discussed above. This latter form occurs over a wide area of the goldfields area of Western Australia and also occurs in the transition zone between the South West Province and the Eremaea, but since species populations in this zone are often highly variable there is a possibility that intergrading specimens will be collected. It is because of this that the two have not been separated at the specific level. The new subspecies is known from the drier parts of the wheat-belt from Mullewa in the north to Lake Grace in the south, and eastwards to Queen Victoria Spring and Israelite Bay (Fig. 5).

The descriptions given by Wheeler and by Goodspeed were evidently based on plants of this subspecies, probably grown from seed collected by Gardner near Lake Grace. A specimen representing this is held at Sydney (Nat. Herb. 48701—ex Univ. Calif. No. 27-1). This agrees with subsp. *aridicola*, though the stems are rather more leafy than is usual in field specimens. Despite this response to what were doubtless better habitat conditions, the stems never become robust as in subsp. *rotundifolia*, and the calyx retains its characteristic features. Cleistogamous flowers are frequently developed in subsp. *aridicola* and in this case the corolla may be little longer than the calyx. In general the trichomes on the pedicels and calyces are shorter, stouter, and thicker-walled than in subsp. *rotundifolia*.

If the species occurs outside Western Australia it is to be expected that it will be represented by this subspecies. The only specimen quoted by Goodspeed which is not from Western Australia is one collected in the MacDonnell Range by Cleland. This represents *N. simulans*, a duplicate held at Adelaide having been examined. It seems probable that other South Australian specimens referred to *N. rotundifolia* all belong with *N. simulans* or are small-flowered plants of *N. velutina*, but not all those on which the remarks in Black's (1957) handbook to the flora of South Australia (2nd Ed.) were based have been examined. The specimen referred to by Cleland and Tindale (1959, p. 138) as *N. rotundifolia* (*Cleland* 38a, Haast's Bluff) has been quoted above under *N. simulans*.

Specimens Examined.—21 miles E. of Pindar, *R. Melville* 4225, 20.vii.1953 (stems glabrous above and flowers larger than usual) (NSW, AD); N. of Tardun, *N. T. Burbidge* 4714, 8.xii.1955 (seed only—glass-house plants under T.S. 199) (CANB); Kellerberrin, *E. H. Vachell*, Dec. 1903; Hines Hill, *M. Koch*, 2.x.1923 (NSW); Parker Ra., *E. Merrill*, 1890 (MEL); Coolgardie, "C. L. Webster 1898 coll. C. Walter" (MEL, NSW): 19 miles S. of Coolgardie, *N. T. Burbidge* 2622, 19.ix.1947; 25 miles S. of Coolgardie, *N. T. Burbidge* 4881, 17.xii.1955 (voucher for T.S. 193); 32 miles S. of Coolgardie on regrowth after burn, *N. T. Burbidge* 4886 (voucher for T.S. 194) and 4889 (voucher for T.S. 197), 17.xii.1955 (CANB); Camp 61 (between Streich Mound and Fraser Ra.), *Helms*, 25.ix.1891; Fraser Ra., *Dempster*, 1874; Israelite Bay, *Miss Brook*, Dec. 1884, also 1885 (MEL); ex. Univ. Calif. No. 27-1—strain originally from Lake Grace, coll. *C. A. Gardner* (NSW, AD).

16. **Nicotiana excelsior** J. M. Black in Trans. Roy. Soc. S. Aust. **50**: 286 (1926); Goodspeed, Genus *Nicotiana* 469 (1954).

A robust leafy species of glabrous or almost glabrous habit and easily recognized by its strikingly decurrent leaves and large flowers in which the corolla limb is almost entire. The seeds are slightly curved and rough in silhouette owing to the sharply raised ridges of the honeycomb reticulation. (Plate 18, Fig. 1.)

It occurs in the gullies of the ranges in central Australia. The only other glabrous species occurring in this part of the continent is *N. ingulba*, in which the plants are less robust, the leaves are not decurrent, and the seeds are curved (C-shaped), with a close pattern of reticulate serpentine wrinkles.

17. **Nicotiana suaveolens** Lehmann in Isis (von Oken) 181, col. 36; also Gen. Nicot. 43 (1818) (non vidi); Goodspeed, Genus *Nicotiana* 460 (1954).

A variable species, widespread in south-eastern Australia from the south-east of South Australia to north-eastern New South Wales (Fig. 1). The variations and the occurrence of diploid (16 pairs) and tetraploid races have been discussed by Wheeler (1935) and by Goodspeed (1954). The geographic distribution of the two chromosome races has not yet been investigated.

The species is recognized by its glabrous or almost glabrous habit, by its broad corolla tube (relative to its length), and by the seeds, which are slightly curved with a reticulum of round-edged serpentine wrinkles. (Plate 18, Fig. 2.) Among specimens from western New South Wales are some with scabrid stems. The corolla size varies greatly, but at present the significance of such variations is not understood.

18. **Nicotiana ingulba** J. M. Black in Trans. Roy. Soc. S. Aust. **57**: 156, pl. 9, fig. 1 (1953); Goodspeed, Genus *Nicotiana* 475 (1954).

A glabrous species of branching habit, leafy stems, and long slender flowers with spreading corolla limb. In the key provided by Goodspeed it is placed with species having an asymmetrically flared throat due to the subdidynamy of the upper stamens. This asymmetry is never conspicuous and is difficult to discern in dried material. The seeds are curved (open or tight C-shape) with a reticulum of round-edged serpentine wrinkles (Plate 19, Fig. 1).

Under poor conditions the plants may be limited to a basal cluster of leaves and a simple raceme of undersized flowers. In such cases it may be necessary to rely on the seed characters and on the lack of spreading hairs on the lower stem to distinguish it from *N. rosulata*.

The majority of specimens examined were from central Australia, from north of the MacDonnell Range and south to the Everard and Birksgate Ranges; but Western Australian specimens collected by Helms from the Victoria Desert (MEL) and from the Fraser Range (NSW) show that it extends further to the south and west (Fig. 3).

19. **Nicotiana exigua** Wheeler in Univ. Calif. Publ. Bot. **18**: 64 (1935); Goodspeed, Genus *Nicotiana* 473 (1954).

This species is not easily distinguished from *N. goodspeedii*, which is discussed below. The type came from southern Queensland, but examination of a number of sheets in the National Herbarium of New South Wales shows that it extends south to central New South Wales, where its distribution impinges on that of *N. goodspeedii* (Fig. 1).

The plants have a well-formed cluster of radical and lower leaves which are elliptical or broadly lanceolate. Close examination shows that these leaves bear minute soft hairs on the margins and main nerves. Similar hairs occur on young shoots. In good specimens these characters, with the ovoid shape of the capsules and the elliptical cauline leaves, serve to separate *N. exigua* from *N. goodspeedii*. The seeds of the two are closely similar, but if comparative specimens are available it can be seen that those of *N. exigua* are neater, with the ends of the tightly curved seeds commonly touching and the reticulation a fine pattern of serpentine wrinkles (Plate 20, Fig. 1).

20. **Nicotiana goodspeedii** Wheeler in Univ. Calif. Publ. Bot. **18**: 63 (1935); Goodspeed, Genus *Nicotiana* 473 (1954).

The type of this species was obtained at Fowler's Bay in South Australia. Specimens of this species usually have a basal rosette of narrow oblanceolate leaves, the cauline ones being similar in shape. The margins and nerves of the leaves are glabrous, or there may be very few minute hairs on the margins at very distant intervals. The capsule is distinctly oblong, not ovoid as in *N. exigua*. The seeds are less tightly curved and have a slightly coarser reticulation (Plate 20, Fig. 2). These differences are adequate when comparing South Australian and Queensland material, but in a number of New South Wales specimens, held at Sydney, the presence or absence of pubescence on the leaf margins was not so readily discerned. If cauline leaves were not well pressed and capsules were absent the placing of the material was difficult. It is possible that the two are not distinct at the specific level, but further detailed field collecting will be necessary before this point can be finally settled.

21. **Nicotiana rosulata** (S. Moore) Domin in Bibl. Bot., Stuttgart, **89**: 592, pl. 36, fig. 11 (1929); *N. suaveolens* var. *rosulata* S. Moore in J. Linn. Soc. **34**: 206 (1898); *N. stenocarpa* Wheeler in Univ. Calif. Publ. Bot. **18**: 61 (1935); Goodspeed, Genus *Nicotiana* 477 (1954).

Holotype.—Wilson's Pool (between Lake Darlot and Mt. Margaret), W.A.. April 1895, *Spencer Moore* (BM, isotype at K).

Holotype of Synonym.—Laverton, Sept. 1909, *J. H. Maiden* (NSW).

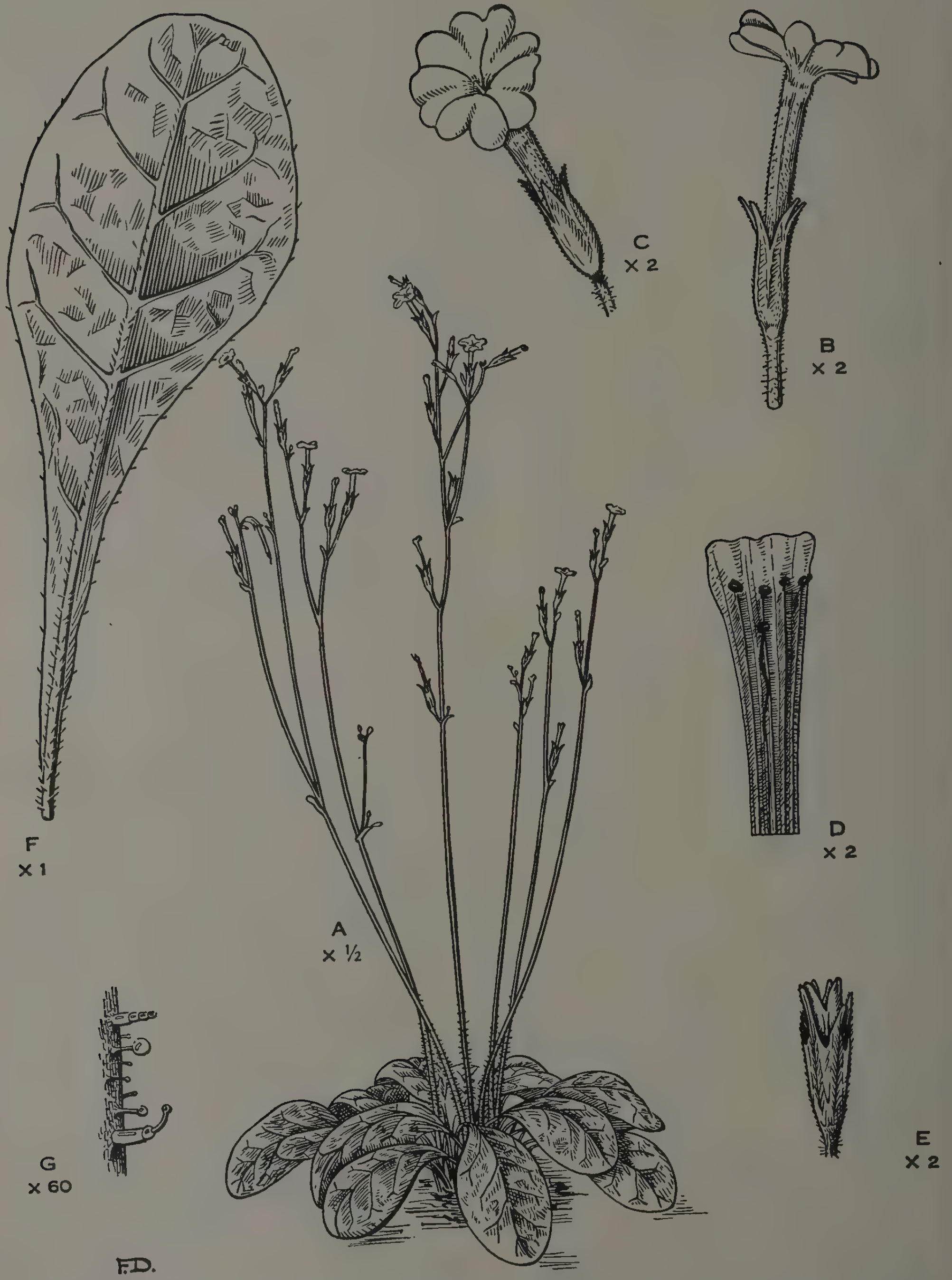
C
× 2
B
× 2
F
× 1
D
× 2
A
× ½
G
× 60
E
× 2
F.D.

Fig. 11.—*N. rosulata* (drawn from glass-house plant of T.S. 184 = *Burbidge* 4858). Lettering as in Fig. 6. *F*, basal leaf.

Plants with a cluster of almost glabrous basal leaves and 1 to several erect stems which have conspicuous, though not dense, spreading hairs in the lower half but are smoothly glabrous above. *Basal leaves* broadly ovate to elliptical or spathulate, pilose when young with spreading hairs on margins and nerves but partially or wholly glabrous later. *Cauline leaves* very few or absent (except in "secondary" regrowth in glass-house plants), narrower and less obtuse than the basal leaves. *Inflorescence* racemose or paniculate, the small linear bracts, pedicels, and flowers minutely glandular pubescent. Trichomes varying in length and mostly with a globular apical cell. *Calyx* cylindrical or narrowly campanulate, the intersepal membranes conspicuous and sometimes broadened above, lobes linear-lanceolate with pale margins. *Corolla* with slender tube 18–30 mm long, delicate in texture, slightly swollen around the upper anthers but not asymmetrically flared, limb well developed. (Wheeler describes the corolla lobes as obtuse, but in specimens examined in both the fresh and dried state they were slightly emarginate. Neither Spencer Moore or Domin comments on this particular feature.) *Upper stamens* in short filaments which are usually somewhat unequal though hardly subdidynamous. *Capsule* fusiform or narrow ellipsoid, usually 9–12 mm long (rarely attaining 13 mm as given by Wheeler). Seeds rough in silhouette, slightly curved, with honeycomb pattern of sharp, slightly irregular ridges. Chromosome number 20 pairs. (Fig. 11; Plate 19, Fig. 2.)

The true position of *N. rosulata* has long been a problem. It was regarded as a synonym of *N. rotundifolia* by Wheeler (1935) and by Goodspeed (1954), but since the latter species is not known to occur as far north as Wilson's Pool, and because both *N. stenocarpa* and the previously unrecognized *N. simulans* occur near the type locality of *N. rosulata*, it was important that the matter be resolved. The figure published by Domin, based on the isotype at Kew, shows a small plant 6–7 cm high with a few basal leaves and a slender stem terminating in one partially open bud and one minute bud initial. Neither the description by Moore nor that by Domin is adequate for critical diagnostic purposes.

At the request of the author, who from field experience was convinced that *N. rosulata* must be the same as either *N. stenocarpa* or *N. simulans*, the material of *N. rosulata* held at Kew and at the British Museum (Natural History) was examined by Dr. R. Melville of Kew, who has kindly provided the following comments: "Coming to the Kew isotype of *N. rosulata*, the proportion of the calyx and corolla are the same as in your T.S. 178, though the absolute size is smaller. This may be due to the diminutive size of the plant, only 2½ inches high. I have not observed any essential difference in the indumentum of T.S. 178, *Burbidge* 145, and the type of *N. rosulata*. If the latter was a hybrid between *N. stenocarpa* and your . . . (manuscript name for *N. simulans*) . . . , I would expect an intermediate indumentum pattern, with some of the hairs of (*N. simulans*) extending up on to the middle regions of the stem. There is no evidence of this. Taking all these facts into consideration, I think *N. rosulata* (S. Moore) Domin is a synonym of *N. stenocarpa* Wheeler. The four upper stamens are out of alignment to about the same degree in all the specimens referred to, so far as I can tell without actual dissection."

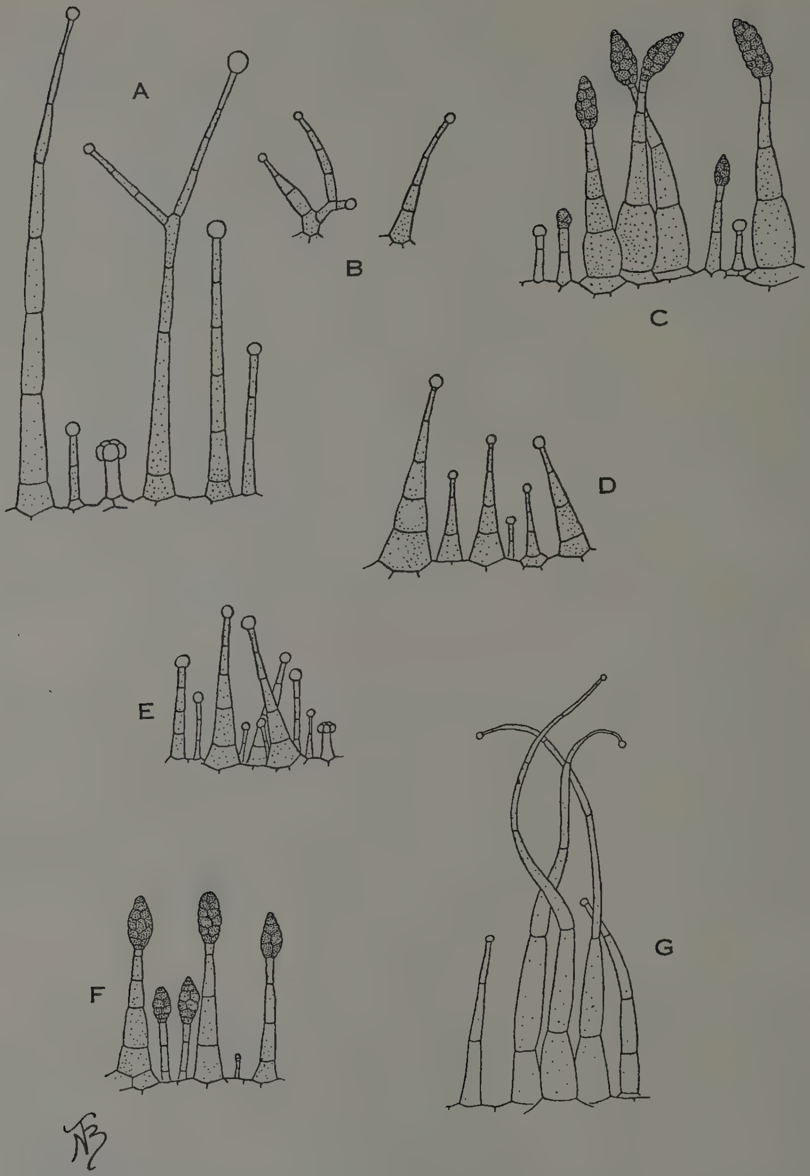

Fig. 12.—Trichomes (all ×50 and, except for *B*, all from pedicels). *A*, *N. rotundifolia* subsp. *rotundifolia*. *B*, *N. rotundifolia* subsp. *rotundifolia* (from calyx lobe). *C*, *N. occidentalis* subsp. *obliqua*. *D*, *N. simulans*. *E*, *N. megalosiphon*. *F*, *N. debneyi*. *G*, *N. gossei*.

T.S. 178 specimens represent glass-house plants grown from seed collected by the author about 9 miles east of Leonora in December 1955. These specimens agree closely with the type of *N. stenocarpa* (which is overmature) apart from slightly shorter capsules. *Burbidge* 145 was collected on Glenorn Station south-east of Malcolm in 1938.

The species is one of the annuals to be found in the patches of ephemeral herbage under the shade of *Acacia* spp. or in litter near fallen branches. It is very commonly associated with *N. simulans*, which flowers at the same time, and it is possible that occasional hybrids occur. These can be suspected when the upper stamens are definitely subdidynamous. Thus in T.S. 308 [glass-house plants grown from seed obtained by the author 45 miles south of Mundiwindi, between Roy Hill and Meekatharra, W.A., 8.v.1958 (*Burbidge* 6067)], in T.S. 313 [glass-house plants], and in its voucher *Burbidge* 6079 [100 miles south of Mundiwindi, 8.v.1958] the flowers have subdidynamous upper stamens and the corolla tube up to 40 mm long. Such plants might be suspected of belonging with *N. ingulba* but for the habit of the plants, the hairs of the lower parts of the stems, and the slender flowers. In T.S. 313 the seeds have a surface pattern as in normal *N. rosulata*, but in T.S. 308 the ridges, though sharply raised, are serpentine. Among southern specimens T.S. 211—from seed obtained near Mt. Russell, west of Wiluna, 12.xii.1955—and T.S. 213—seed obtained 32 miles south of Wiluna, 13.xii.1955 (both collections by the author) have large flowers with irregularly placed upper stamens and the tube slightly bent at the throat.

The species appears to be widespread in the Eremaean Province of Western Australia but has not, as yet, been collected in central Australia (Fig. 3). A large number of seed samples were obtained in December 1955 but since the plants had dried off it was not possible to collect voucher material. This material has been grown in the glass-house and the specimens, with the original locality and collecting number, are given below.

Specimens Examined.—T.S. 211—*N. T. Burbidge* 4795, Mt. Russell, W. of Wiluna, plain in mulga country, 12.xii.1955; T.S. 213—*N. T. Burbidge* 4811, 32 miles S. of Wiluna, 13.xii. 1955; T.S. 217—*N. T. Burbidge* 4823, 4 miles S. of Lawlers, 14.xii.1955; T.S. 218—*N. T. Burbidge* 4829, 14-Mile Creek, S. of Lawlers, 14.xii.1955; T.S. 174—*N. T. Burbidge* 4842, 17 miles N. of Leonora, in shade of *Acacia* along small watercourse, 14.xii.1955; T.S. 178—*N. T. Burbidge* 4846, 9 miles E. of Leonora on Malcolm road, shaded places under trees in small watercourse, 14.xii.1955; T.S. 221—*N. T. Burbidge* 4852, 18 miles W. of Laverton, under mulga in open country, 15.xii.1955; T.S. 184—*N. T. Burbidge* 4858, 8 miles W. of Laverton, under mulga, 15.xii.1955; T.S.185—*N. T. Burbidge* 4863, 1½ miles S. of Malcolm, small creek with *Acacia* spp., 16.xii.1955; T.S. 189—*N. T. Burbidge* 4868, 4 miles S. of Melita turn-off on Leonora–Menzies road, small watercourse in mulga country, 16.xii.1955; T.S. 190—*N. T. Burbidge* 4869, 21 miles S. of Melita turn-off, small watercourse in mulga country, 16.xii.1955 (CANB).

ACKNOWLEDGMENTS

Acknowledgments are due to a number of officers of the Division of Plant Industry. Special thanks are owed to Mr. A. V. Hill, under whose supervision all of the glass-house material was grown and to whom the author is indebted for his willing cooperation on all occasions. Five of the figures were drawn by Mr. F. Dandridge. The photographs were prepared by Mr. E. Slater. A number of chromosome counts, including those of *N. cavicola* and *N. umbratica*, were made by Dr. C. Barnard.

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EXPLANATION OF PLATES 1–20

PLATE 1

N. benthamiana Type sheet, Herb. Kew.

PLATE 2

N. benthamiana Clement specimen from between Ashburton and Yule Rivers, Herb. Kew. Specimen on the right is of *N. occidentalis* subsp. *occidentalis*.

PLATE 3

N. benthamiana T.S. 299 from Ord River, Kimberley, W.A. Glass-house plant, showing strong main shoot and slender basal laterals.

PLATE 4

Fig. 1.—*N. benthamiana* T.S. 318 from Mundbullangana, south of Port Hedland, W.A. Note axillary flowering shoots and flowers on main shoot (a large-flowered individual).

Fig. 2.—*N. benthamiana* C.P.I. 21181, received from U.S. Department of Agriculture. Note early stages in development of flowering laterals.

PLATE 5

Fig. 1.—*N. rotundifolia* subsp. *rotundifolia* (glass-house plant).

Fig. 2.—*N. rotundifolia* subsp. *aridicola* (glass-house plant of T.S. 194 = *Burbidge* 4886).

PLATE 6

Fig. 1.—*N. rotundifolia* subsp. *rotundifolia* (plant of T.S. 196 showing secondary type growth). Note some pedicels recurved.

Fig. 2.—Flowers of plant shown in Plate 5, Fig. 2.

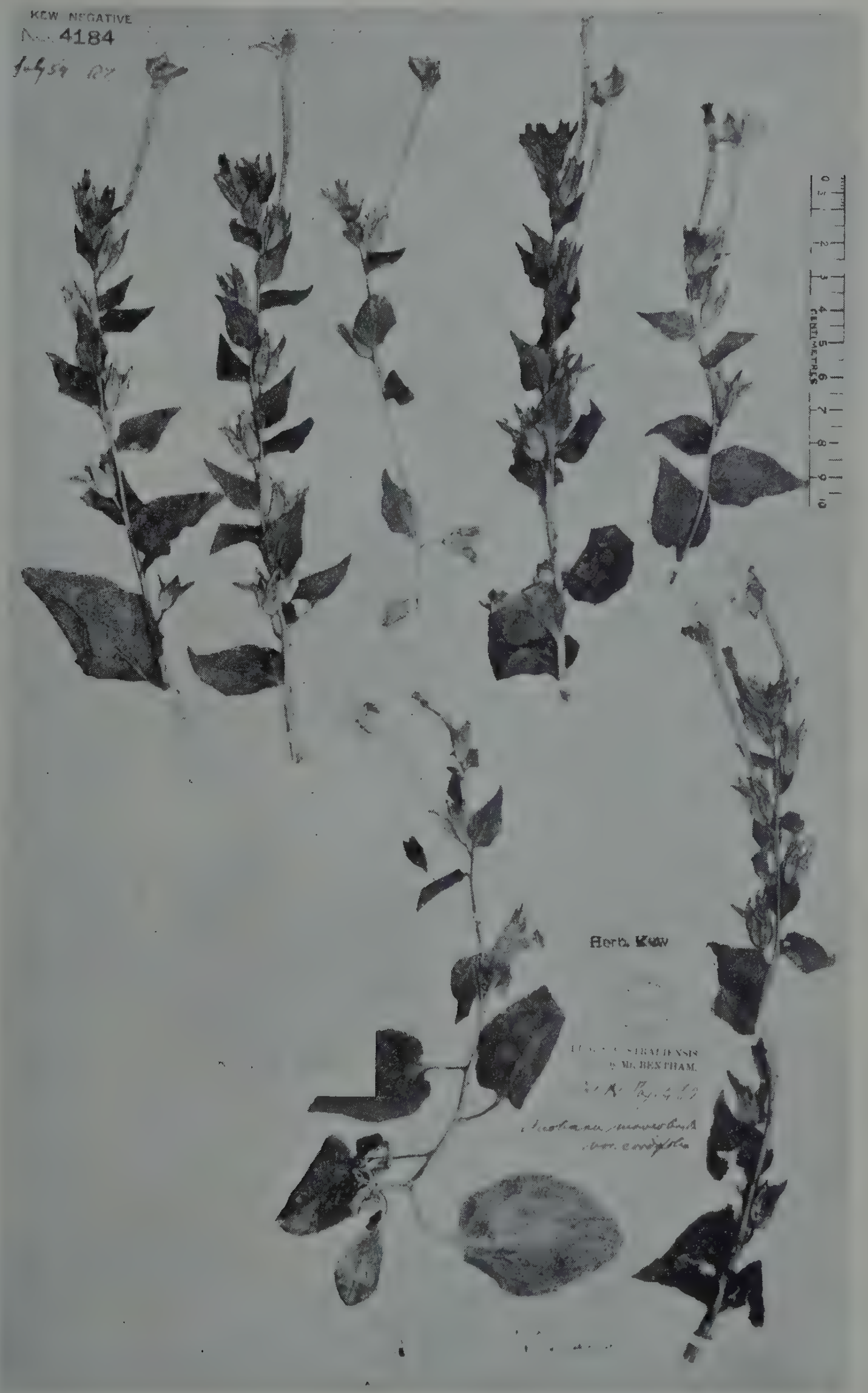
PLATE 7

Branches of inflorescence from upper (Fig. 1) and lower (Fig. 2) portions of plant in Plate 6, Fig. 1.

PLATE 8

Fig. 1.—Buds of *N. megalosiphon* (from glass-house plant of T.S. 158 = Burbidge 4232). Note slight swelling around upper stamens and slight constriction at base of limb.

Fig. 2.—Buds of *N. occidentalis* subsp. *obliqua* (from glass-house plant of T.S. 234). Note asymmetrical throat and lack of constriction at base of limb.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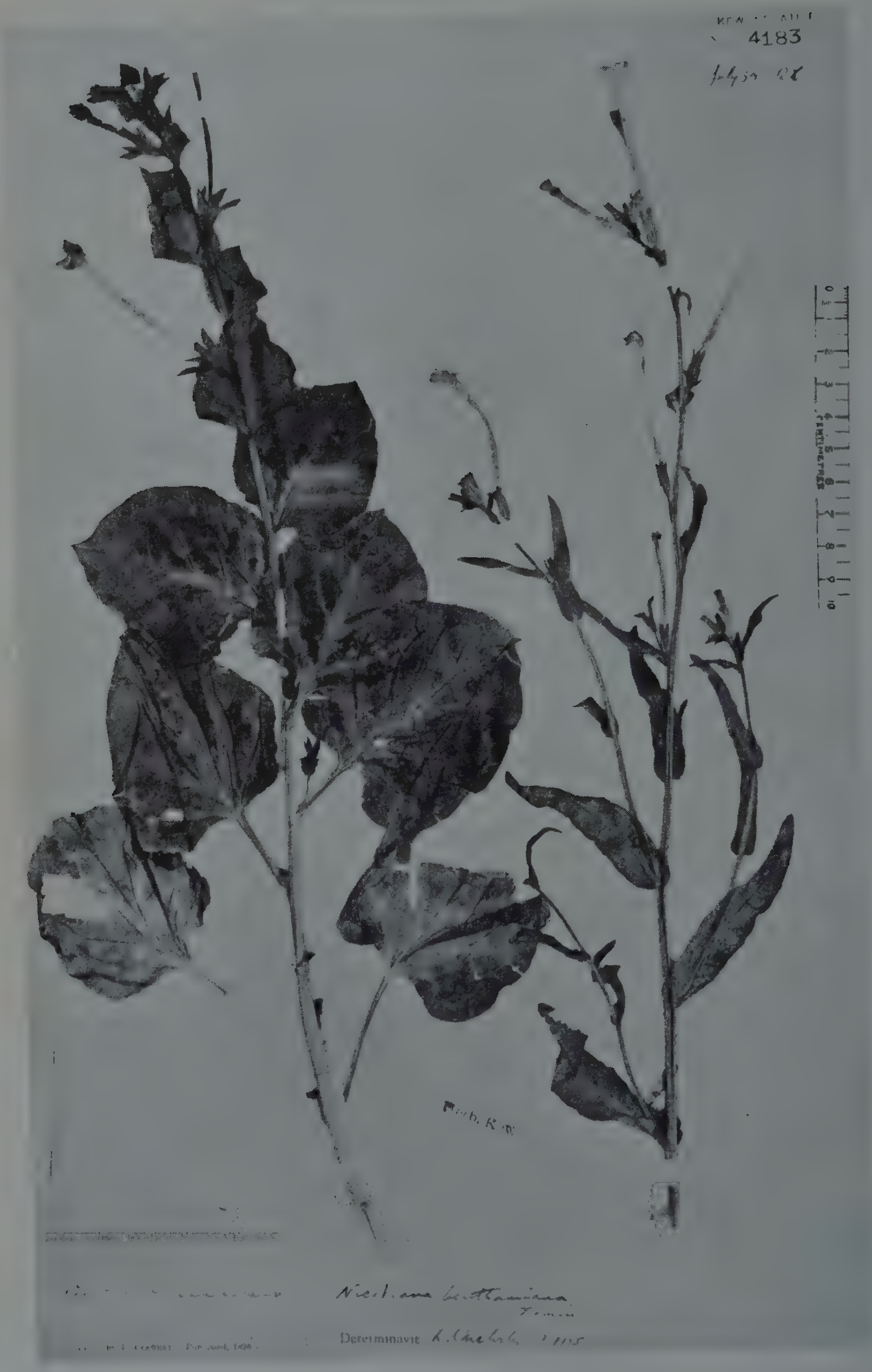
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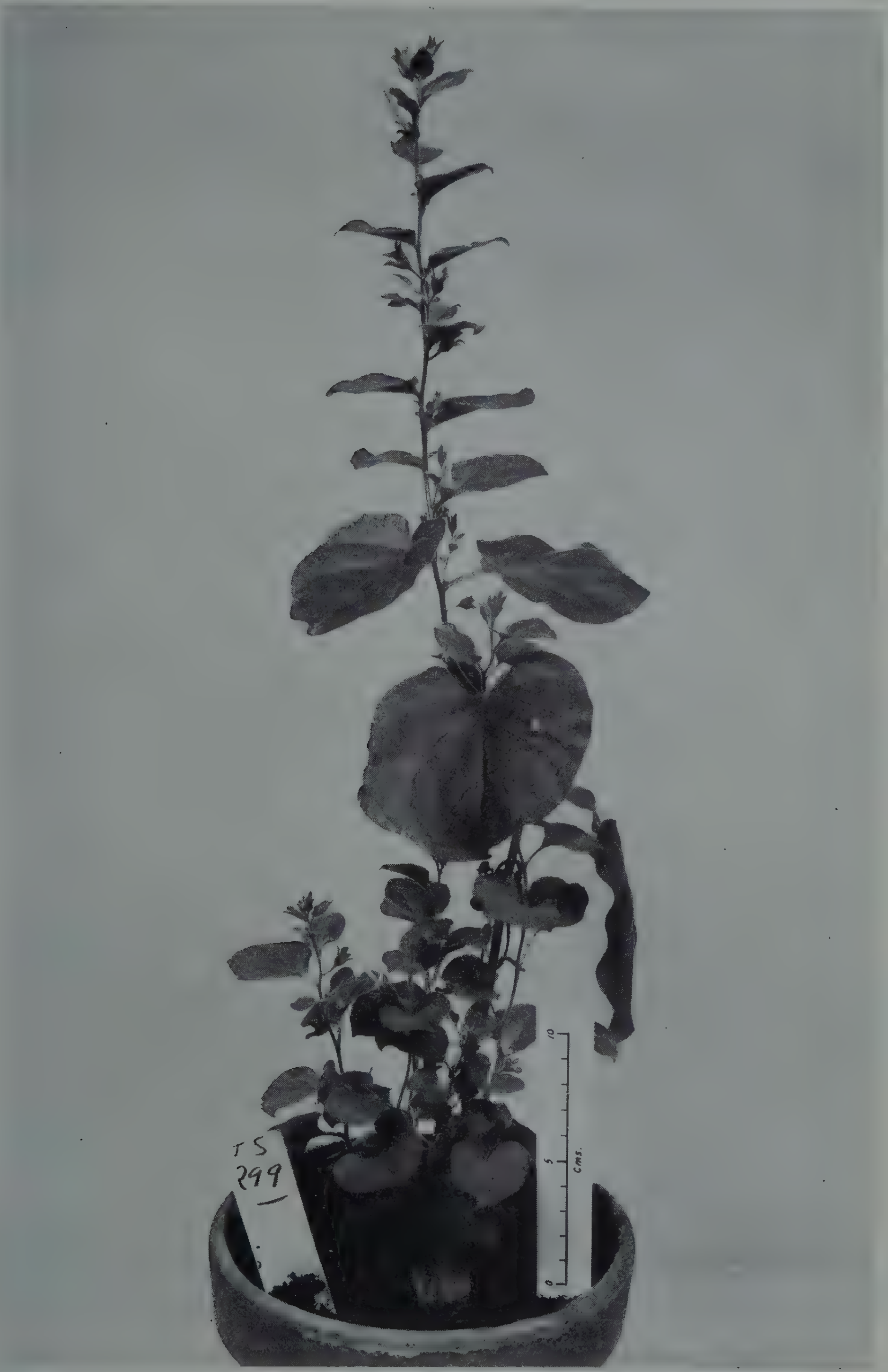
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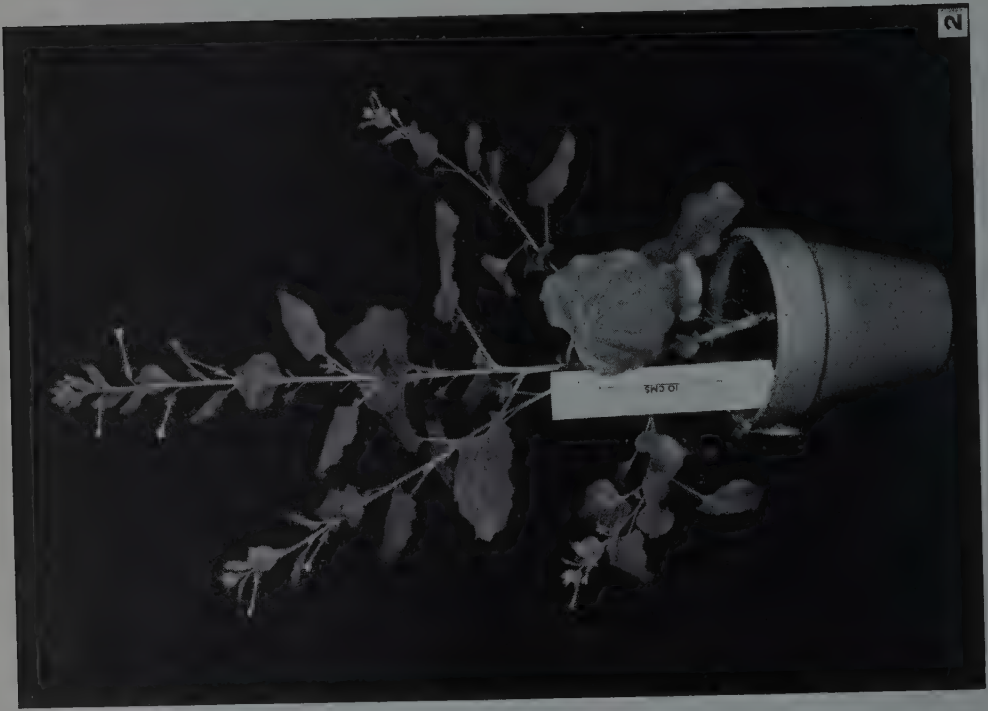
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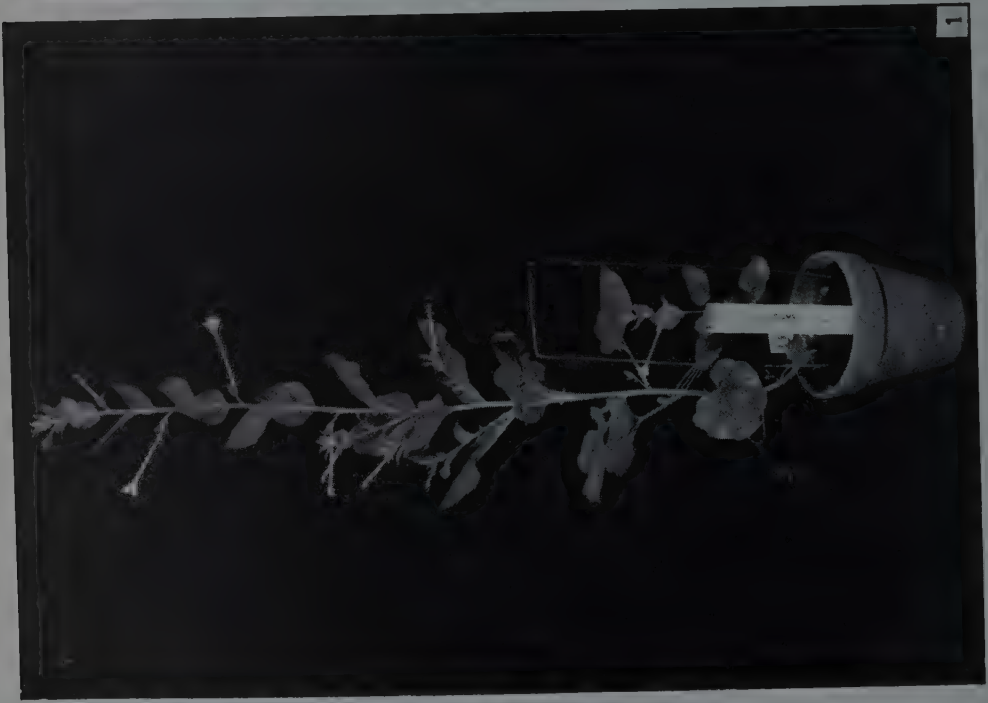
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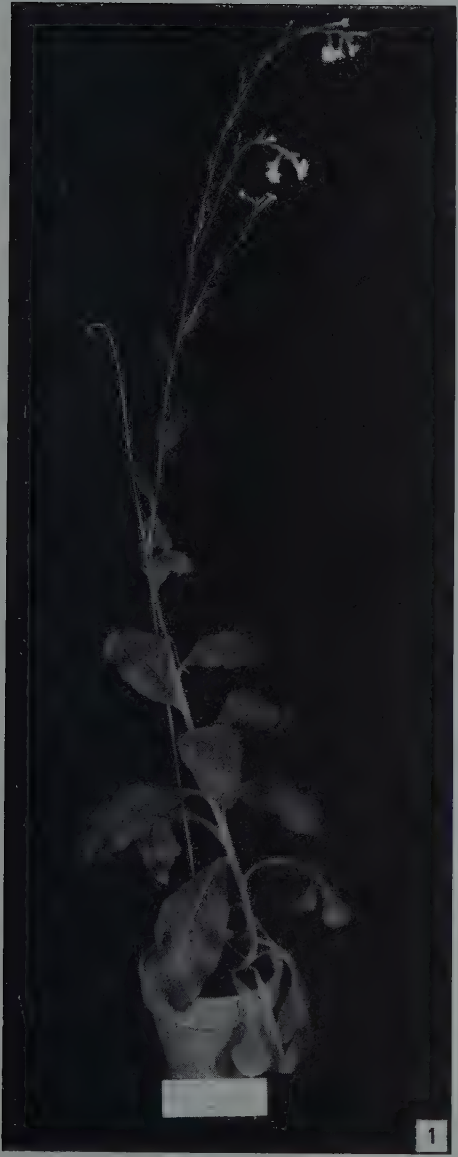

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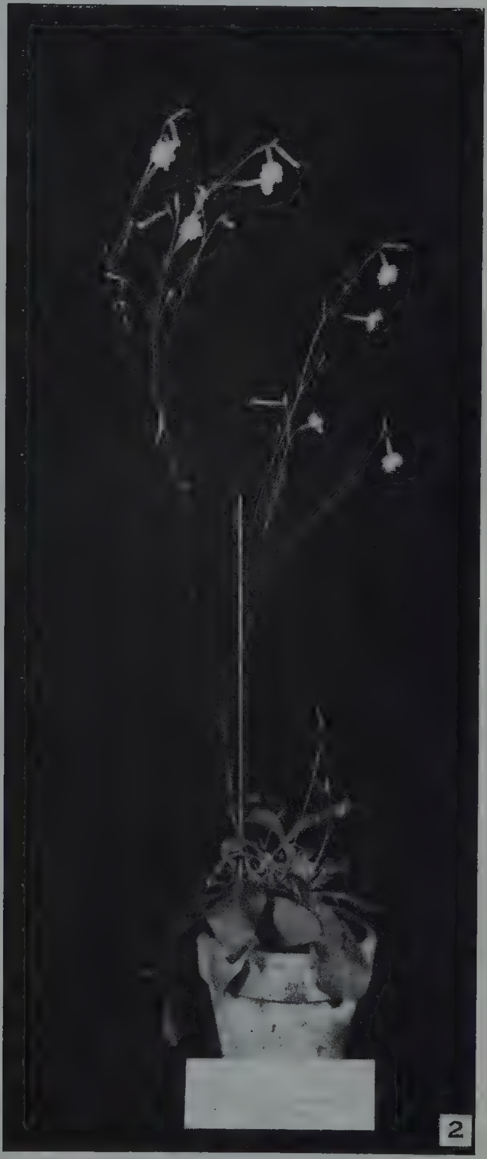

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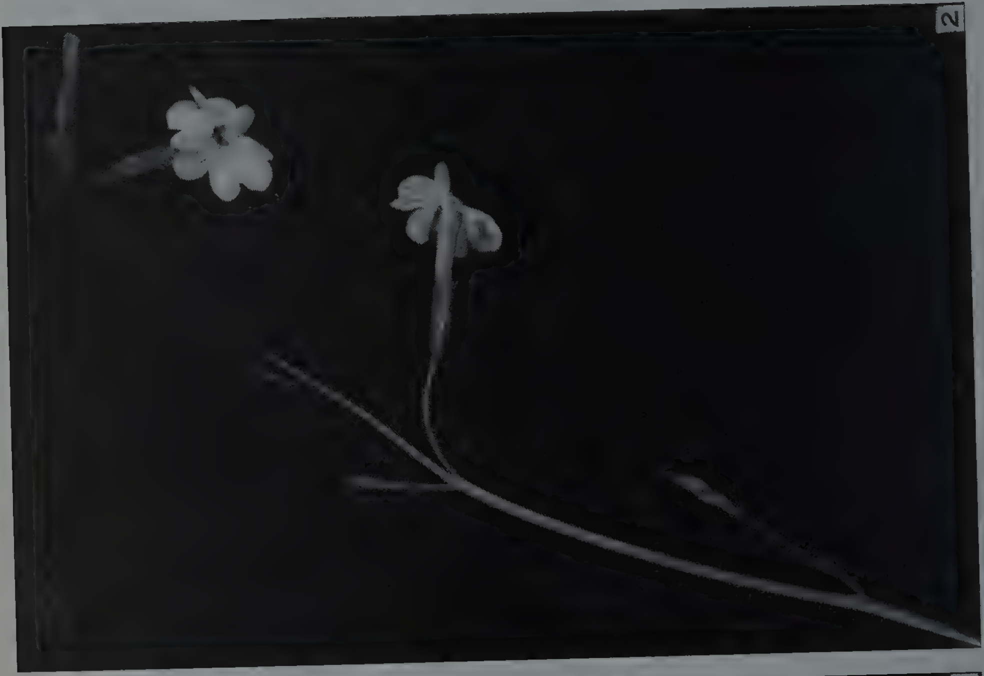

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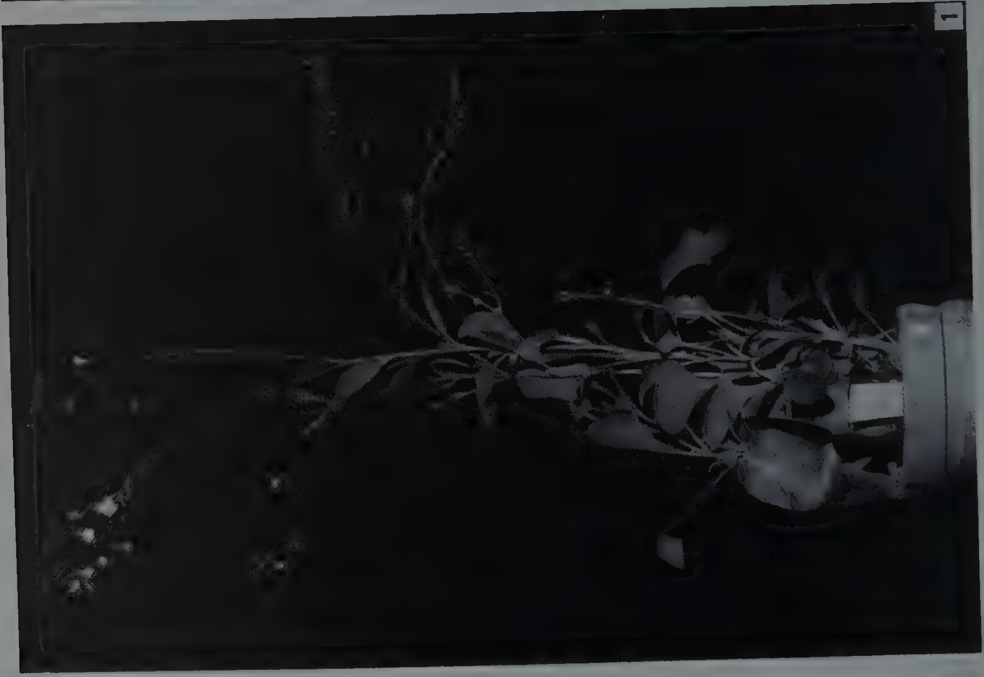

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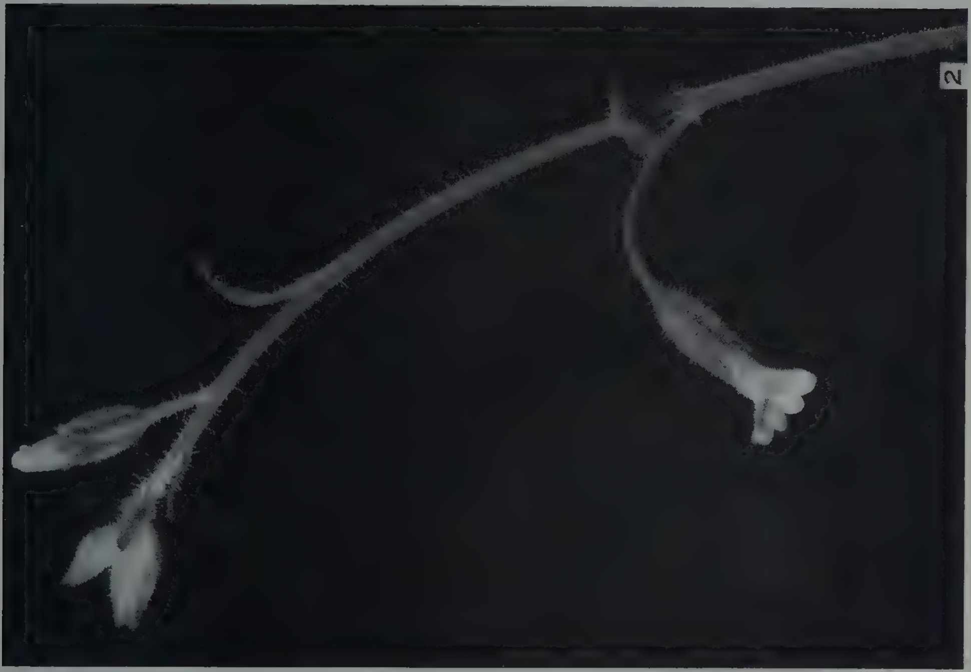

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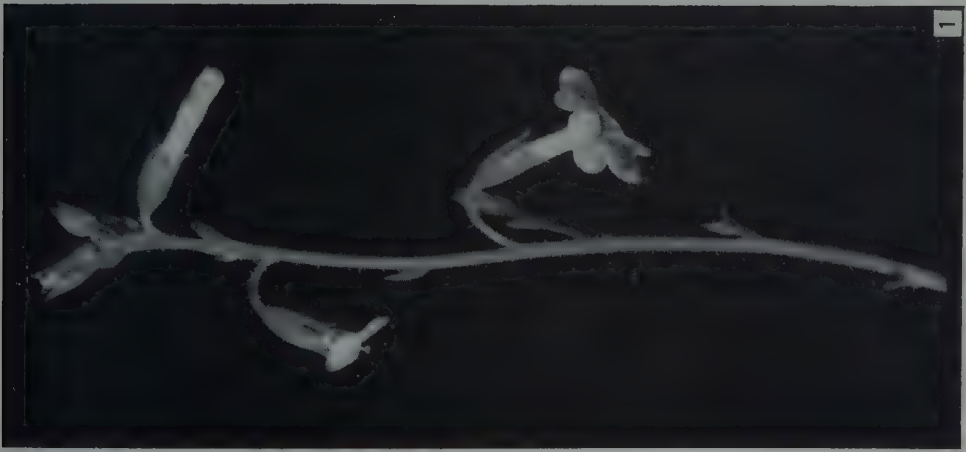

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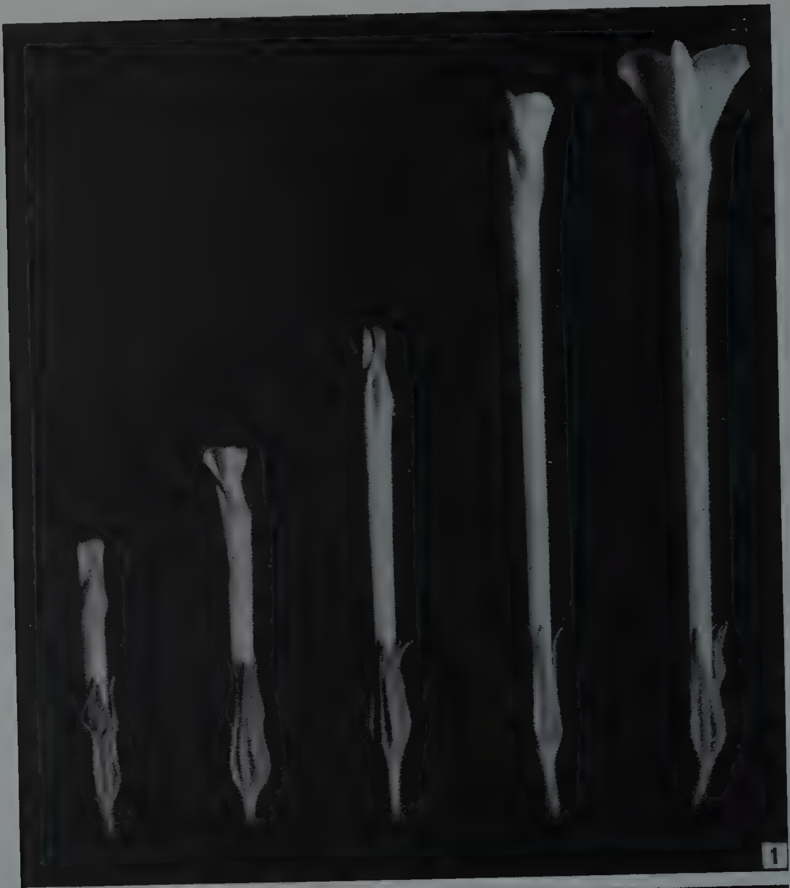

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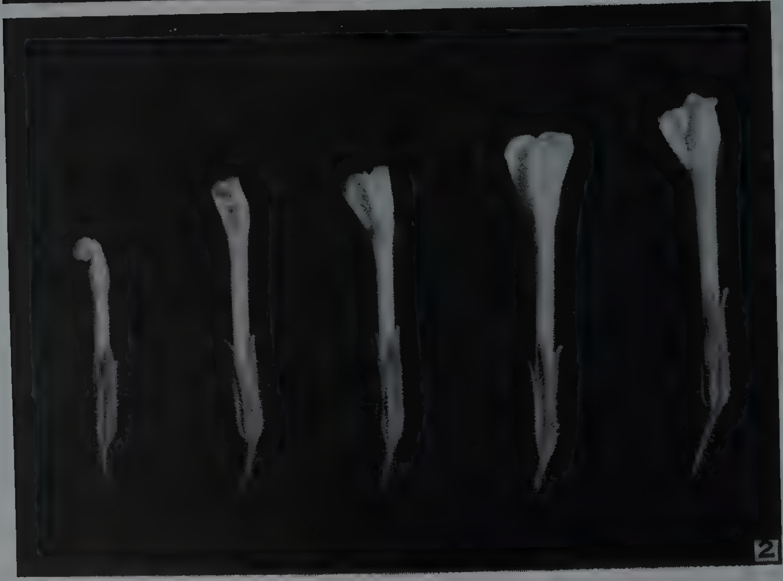

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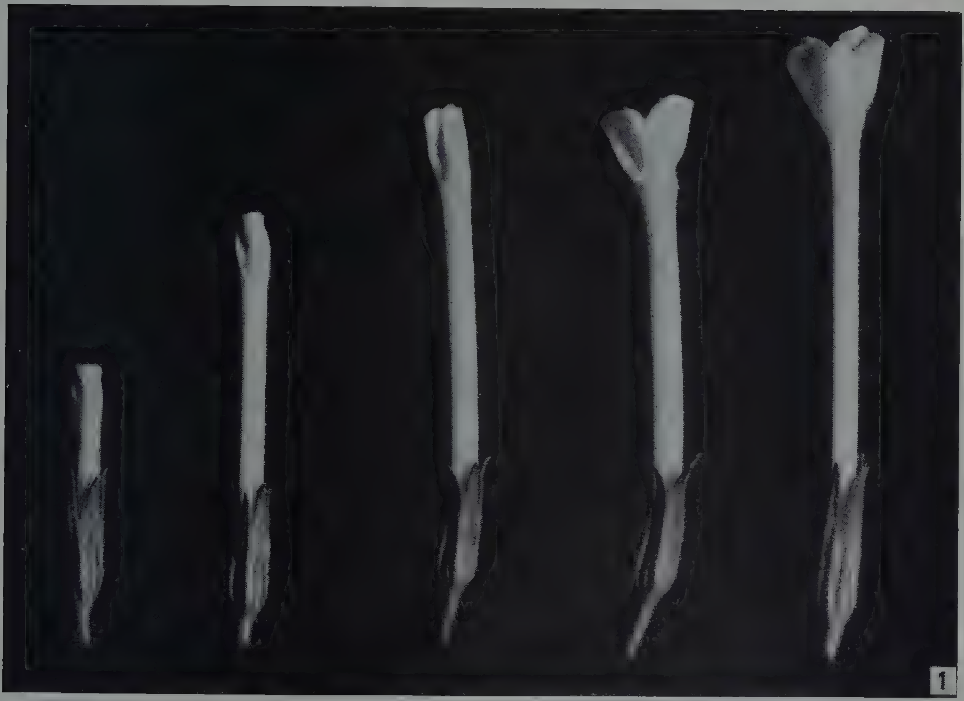
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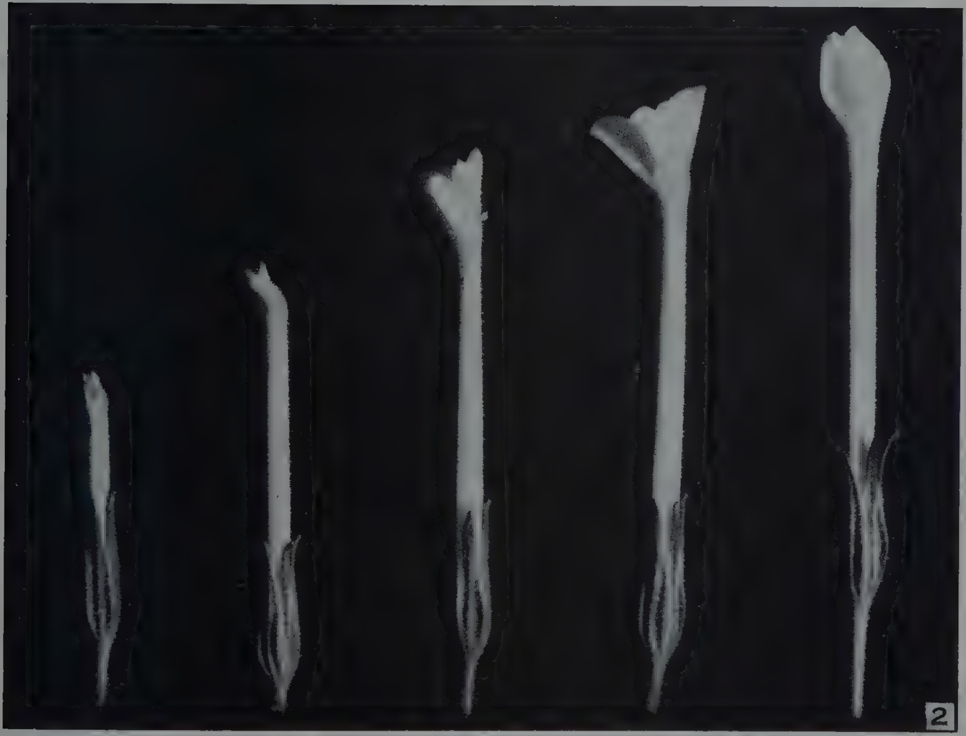
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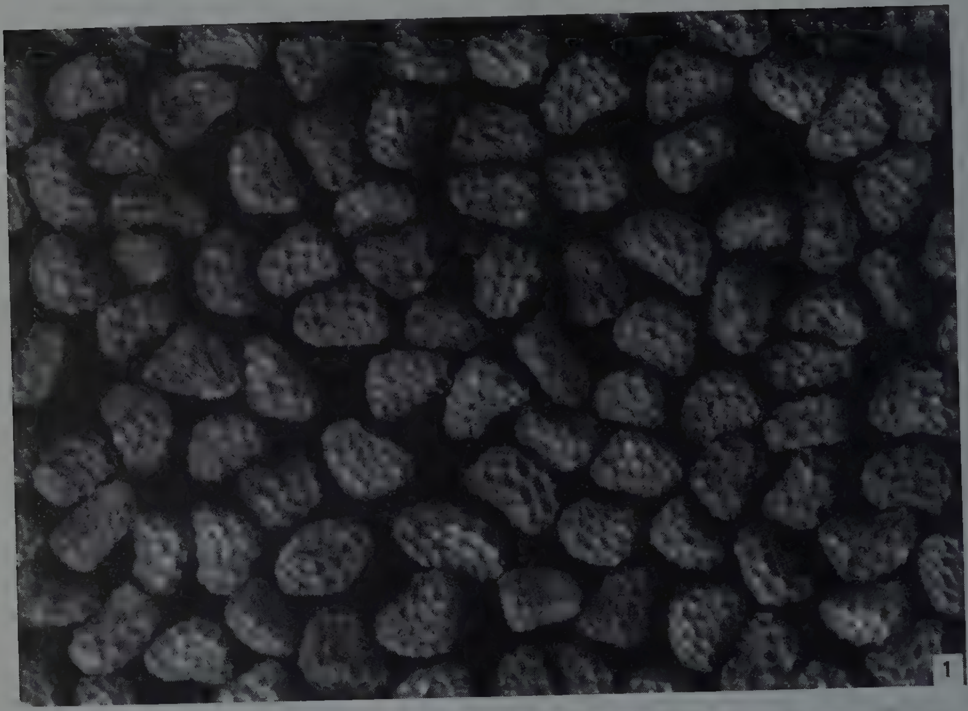

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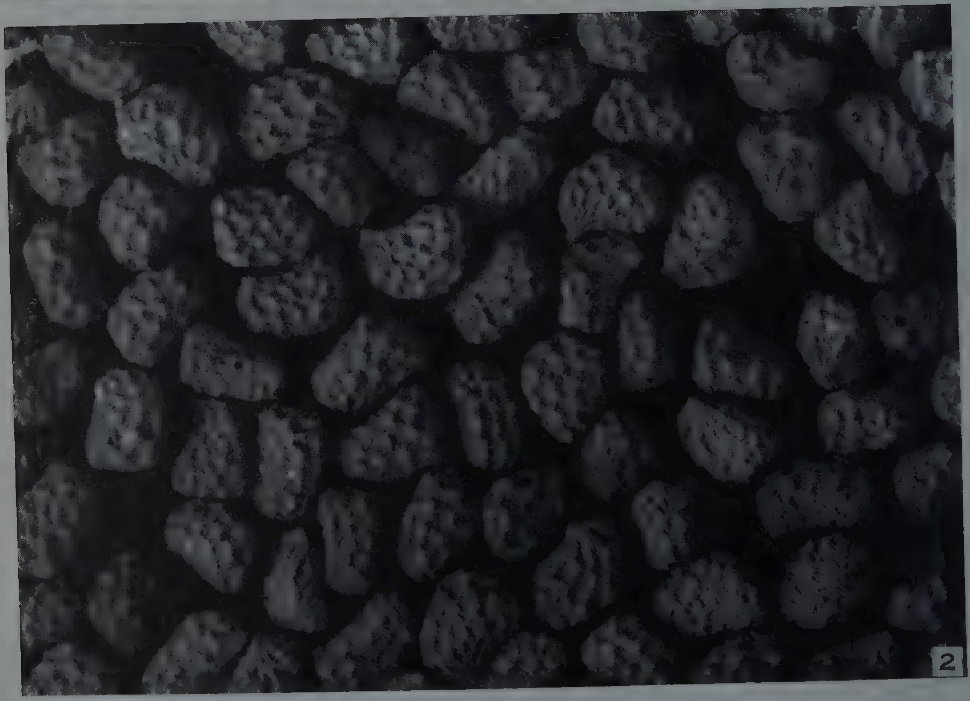

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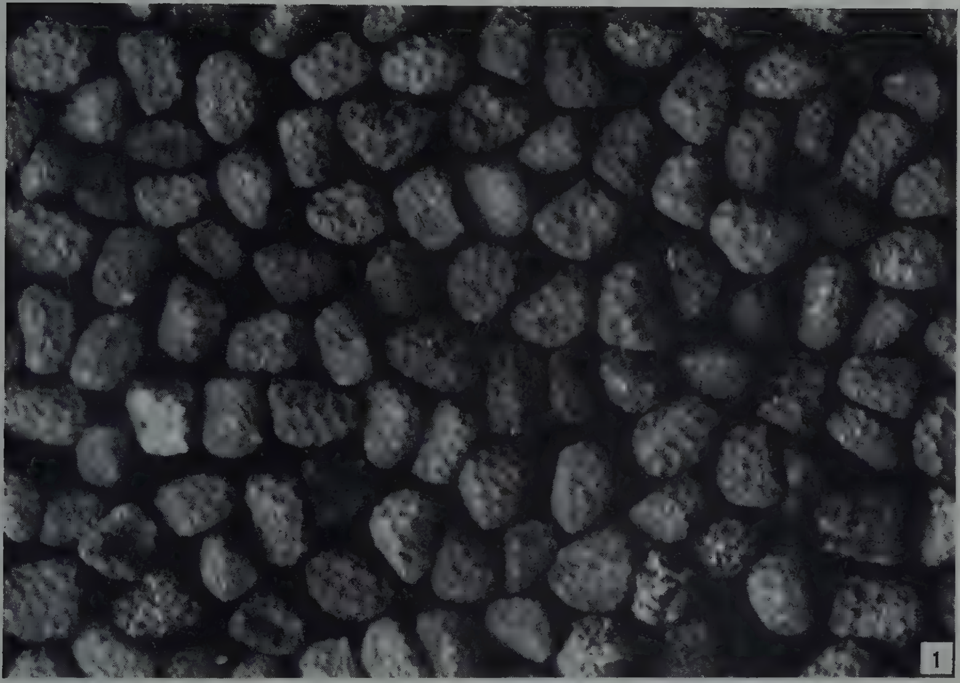
AUSTRALIAN SPECIES OF NICOTIANA



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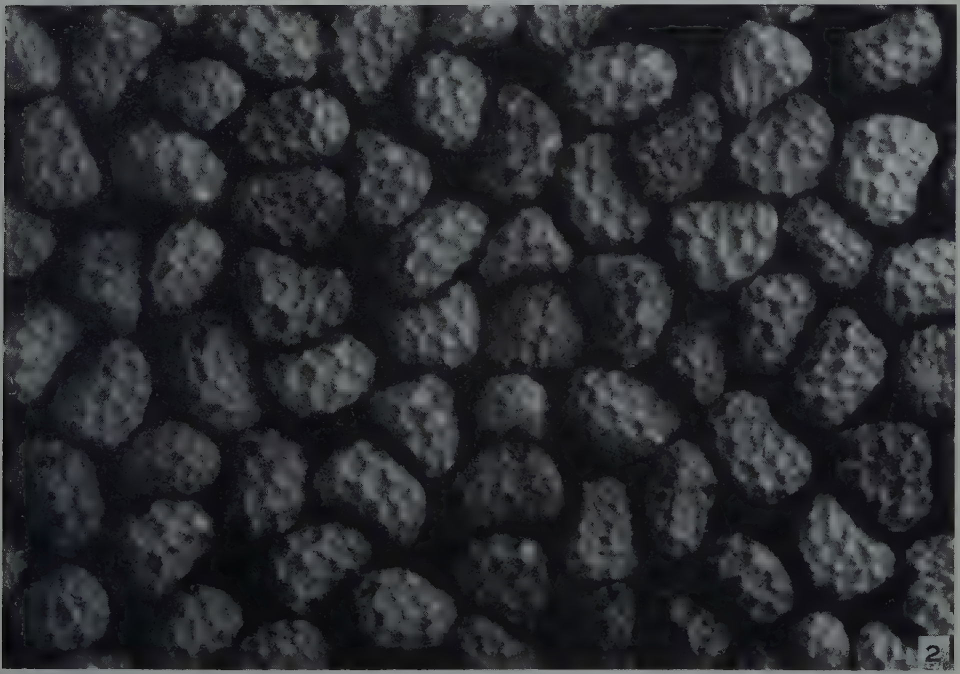

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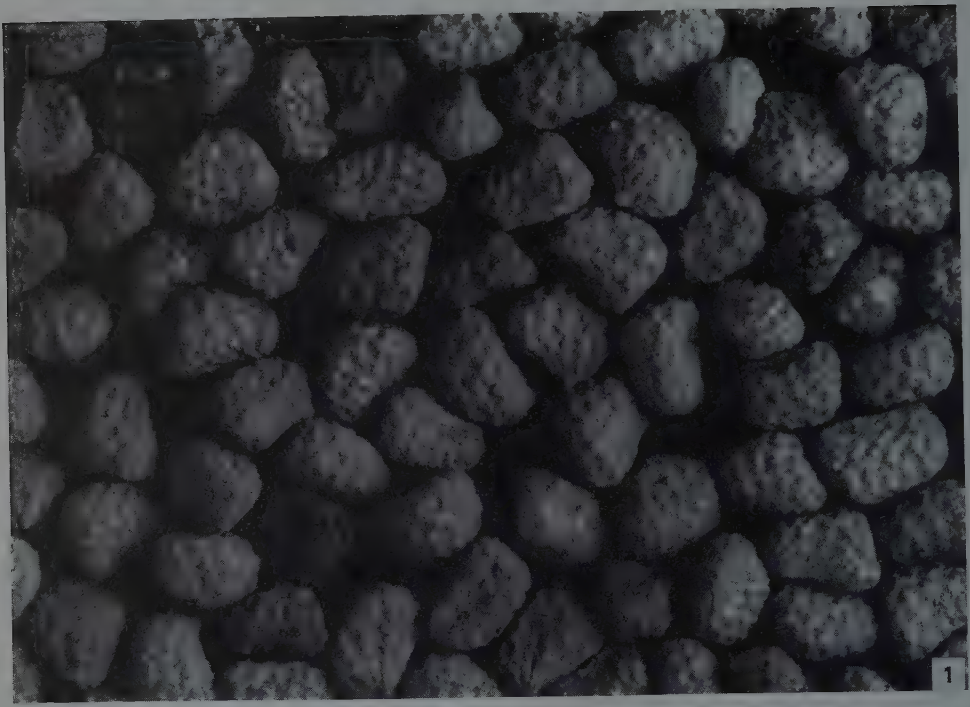
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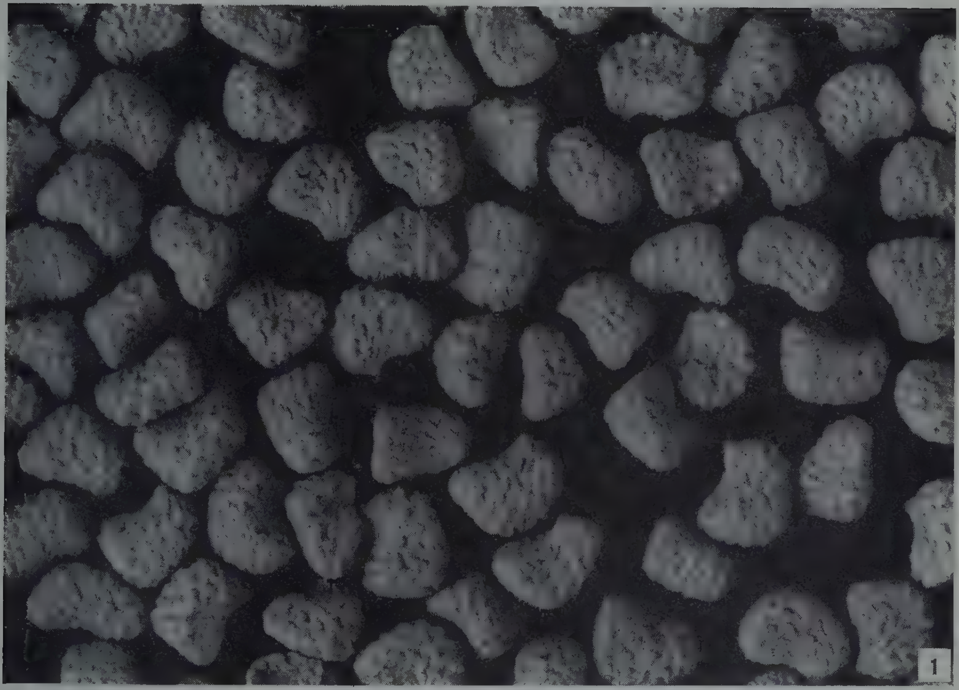
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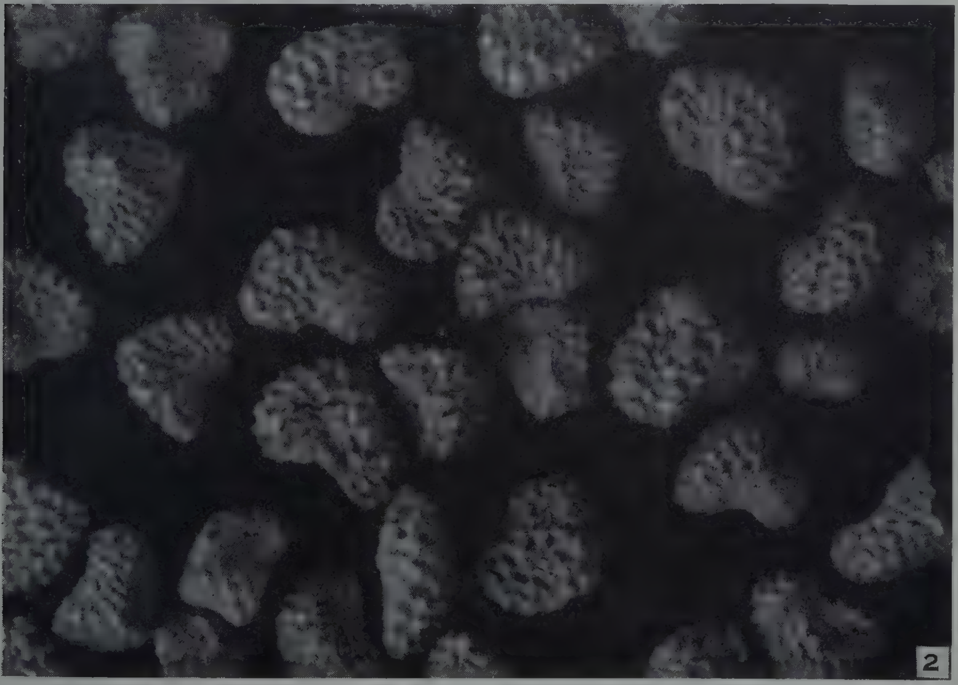
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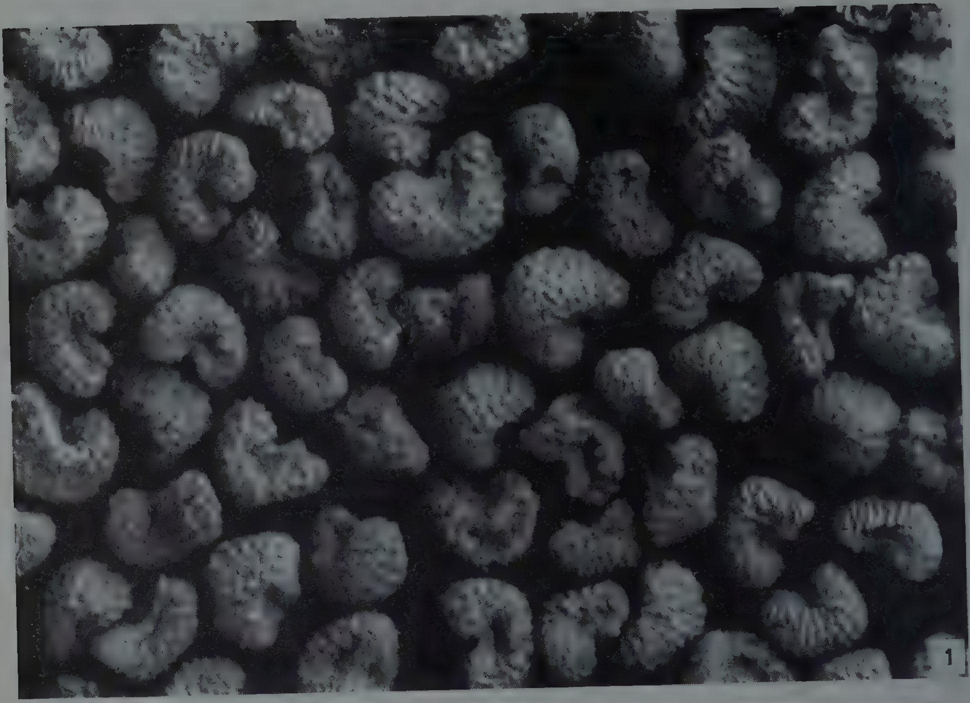

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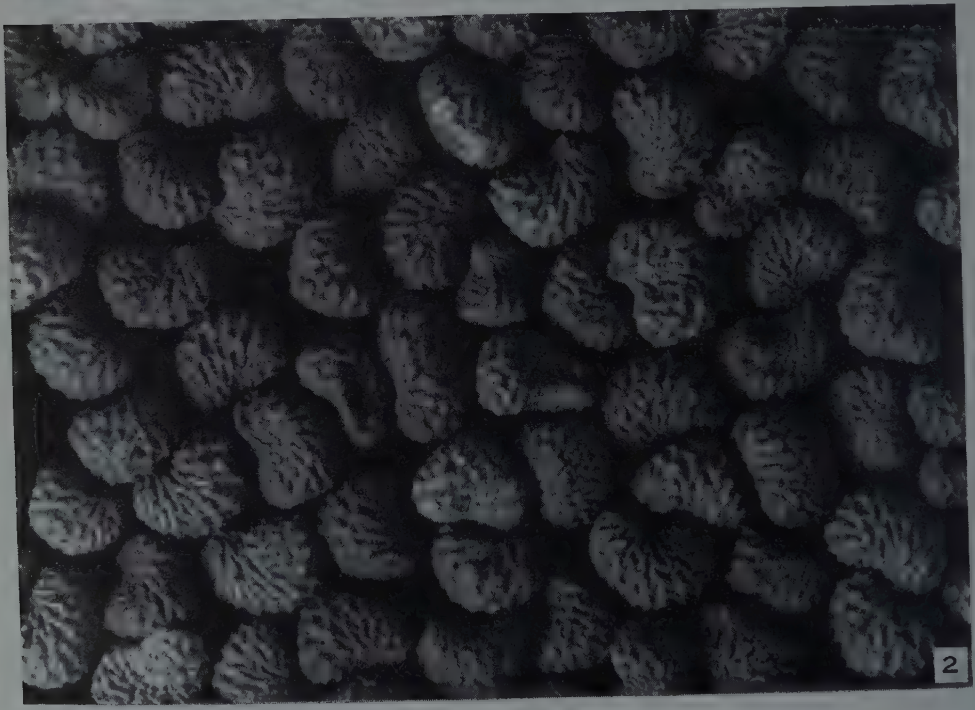

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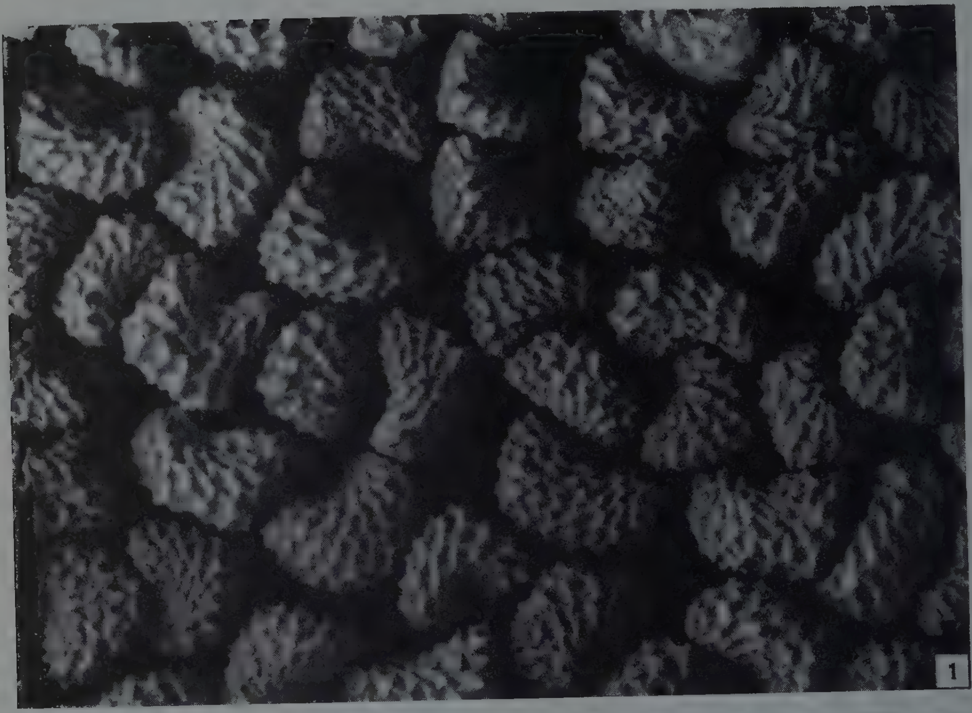

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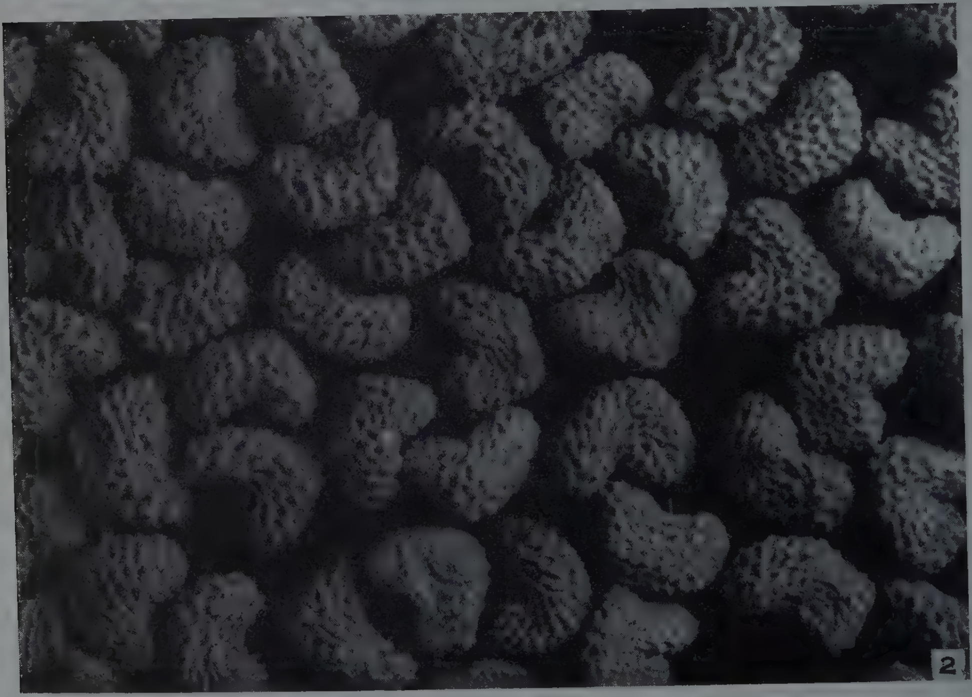

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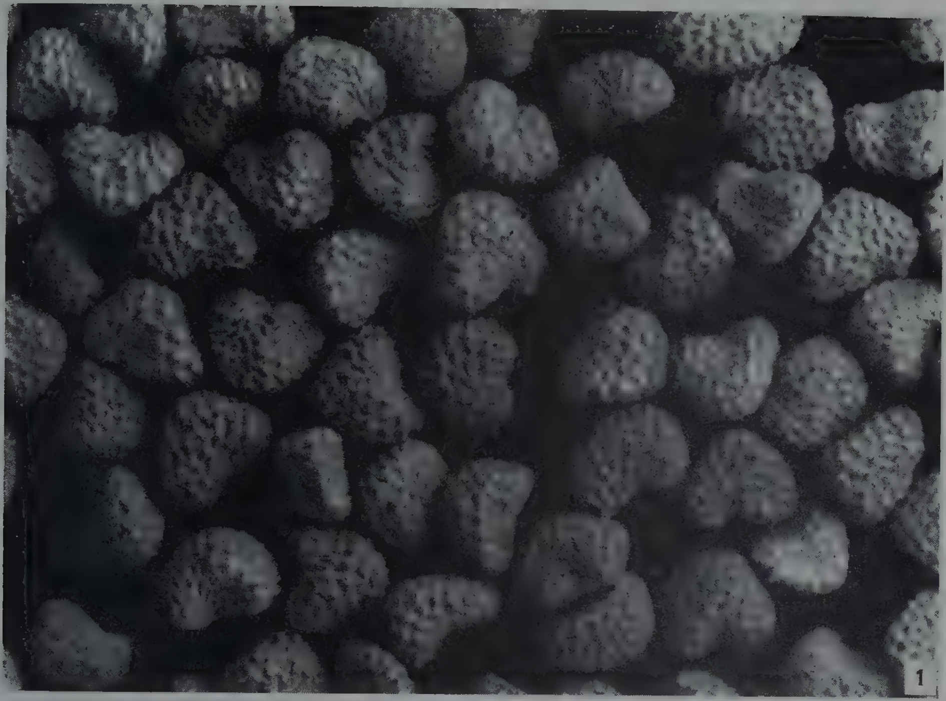
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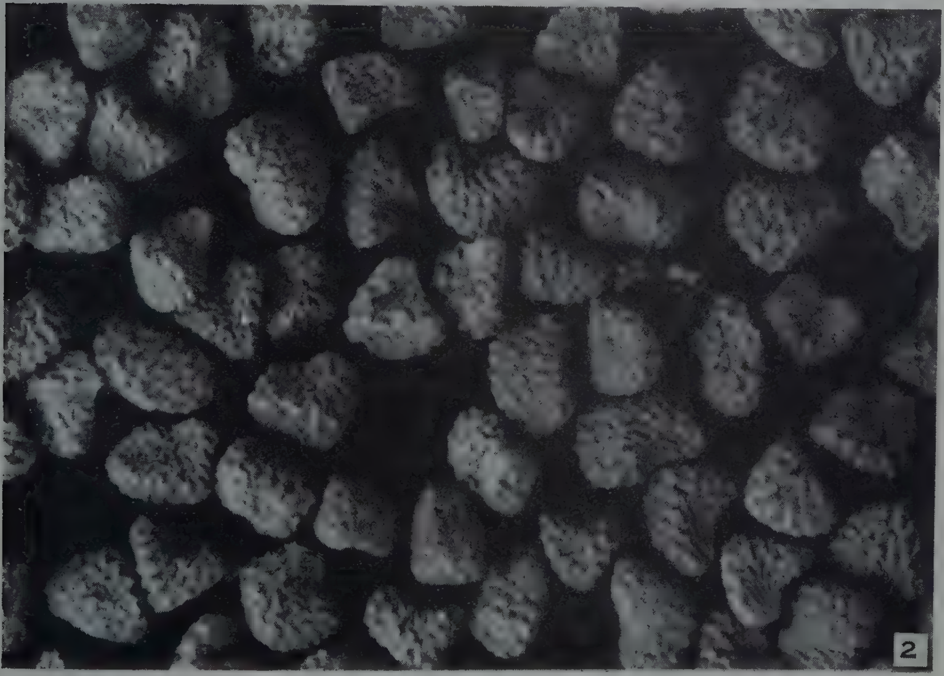
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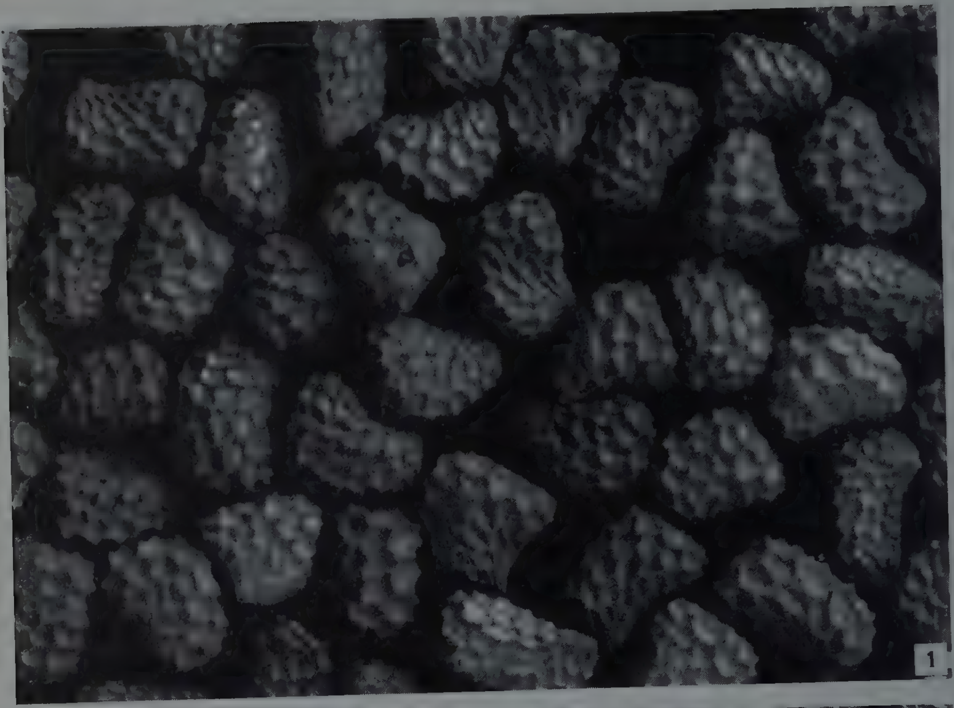

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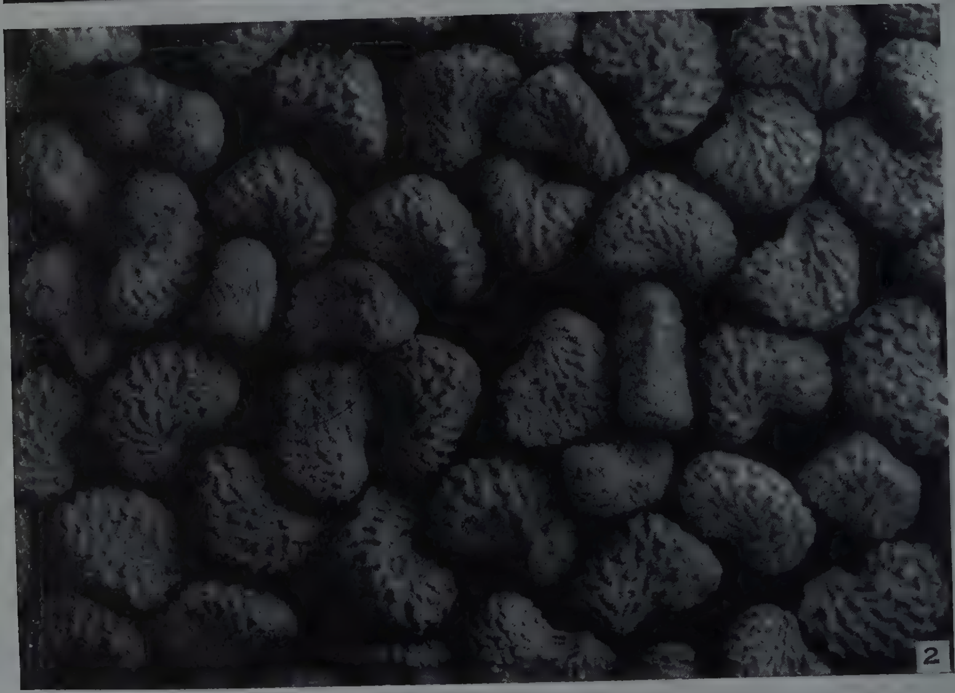

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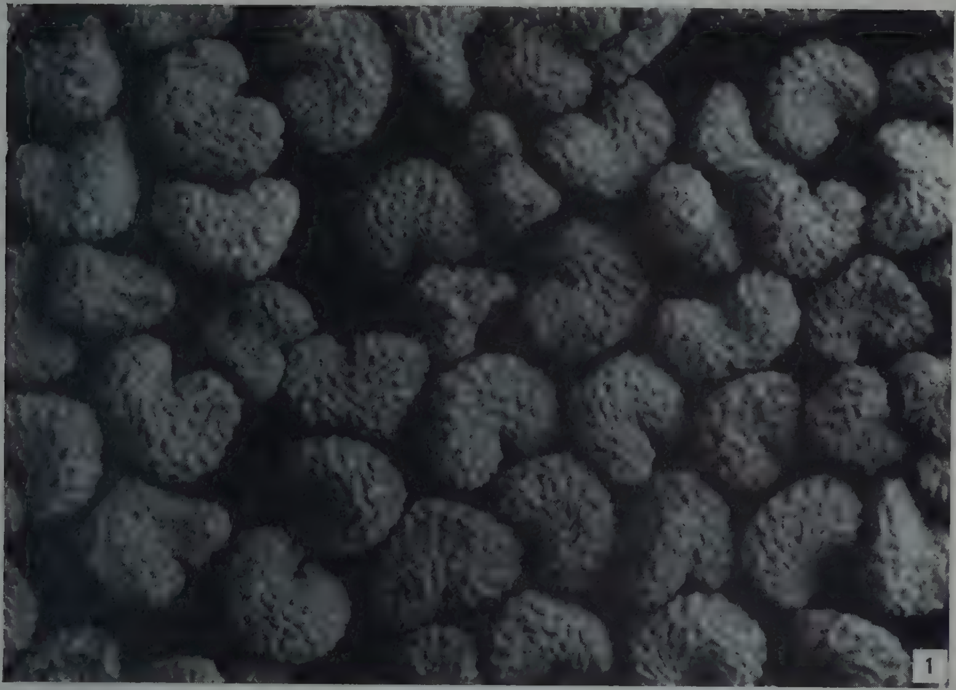
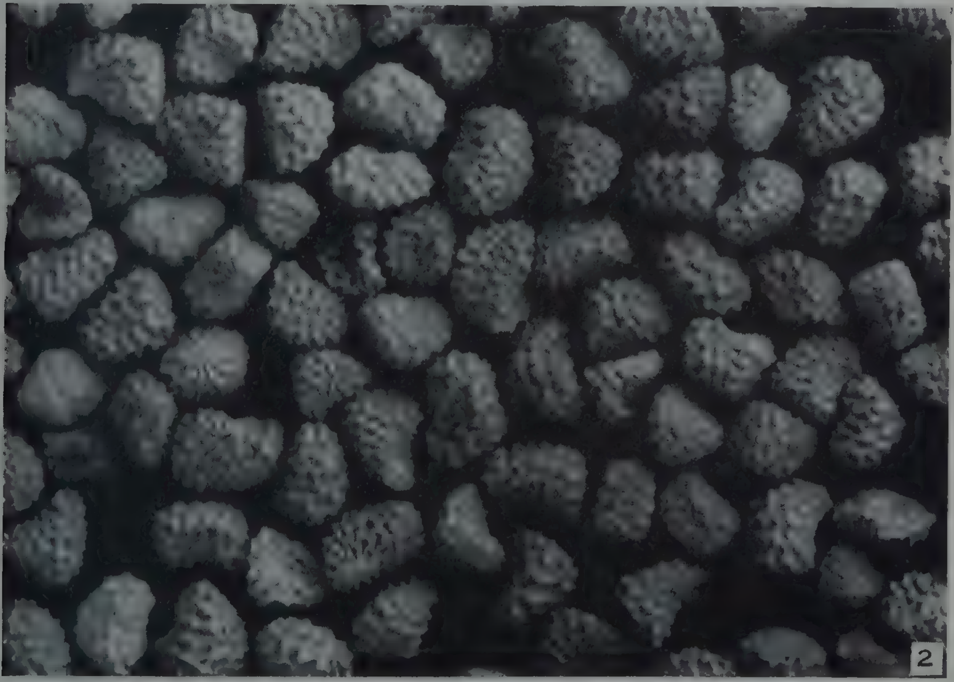
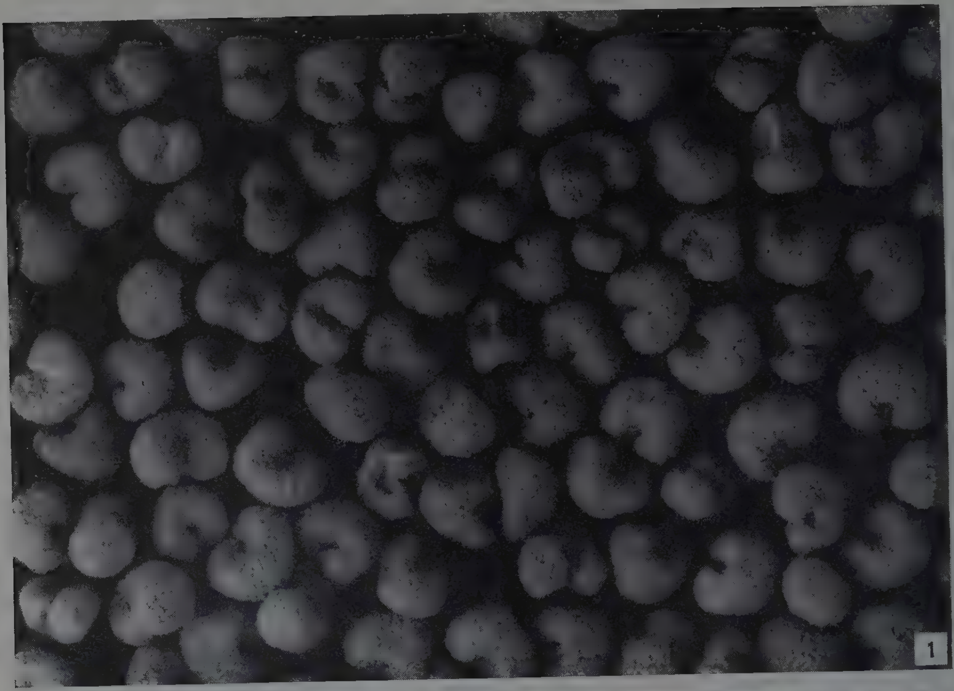
AUSTRALIAN SPECIES OF NICOTIANA







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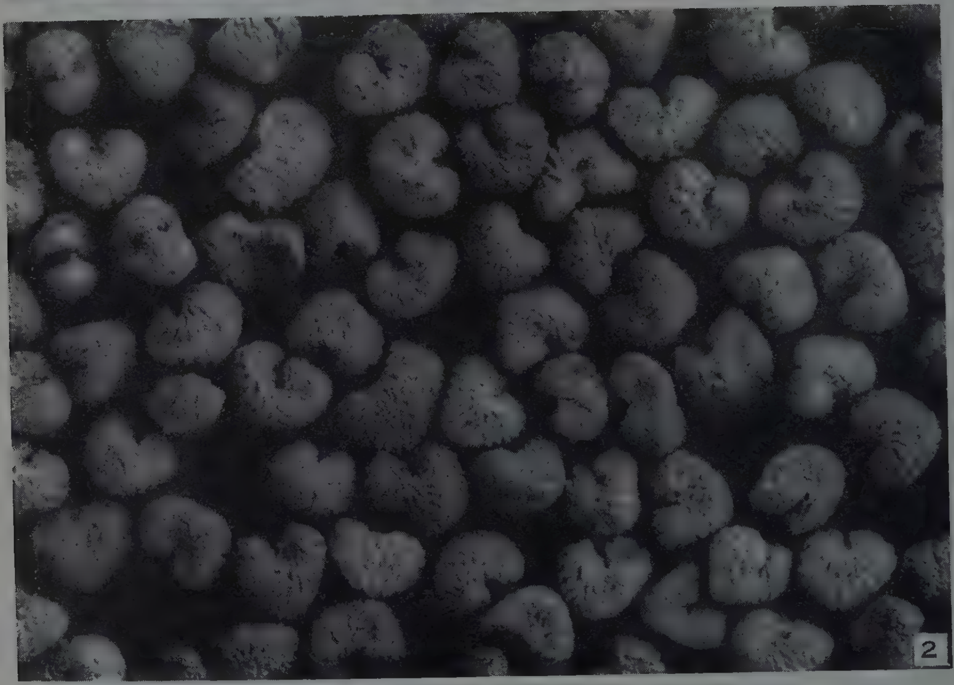

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PLATE 9

Buds of *N. simulans*

Fig. 1.—From plant of T.S. 238 = *Burbidge* 4177.

Fig. 2.—From plant of T.S. 309 = *Burbidge* 6068. "Bud" on the right is a flower in the relaxed daytime position.

PLATE 10

Fig. 1.—Seeds of *N. benthamiana* (T.S. 299). ×20.

Fig. 2.—Seeds of *N. benthamiana* (T.S. 318). ×20.

PLATE 11

Fig. 1.—Seeds of *N. umbratica* (T.S. 302). ×20.

Fig. 2.—Seeds of *N. cavicola* (T.S. 202). ×20.

PLATE 12

Fig. 1.—Seeds of *N. debneyi* (T.S. 233). ×20.

Fig. 2.—Seeds of *N. gossei* (T.S. 74). ×20

PLATE 13

Fig. 1.—Seeds of *N. amplexicaulis* (T.S. 111). ×20.

Fig. 2.—Seeds of *N. maritima* (T.S. 99). ×20.

PLATE 14

Fig. 1.—Seeds of *N. velutina* (T.S. 147). ×20.

Fig. 2.—Seeds of *N. occidentalis* subsp. *obliqua* (T.S. 182). ×20.

PLATE 15

Fig. 1.—Seeds of *N. hesperis* (*Burbidge* 6494) not crested. ×20.

Fig. 2.—Seeds of *N. hesperis* (*Burbidge* 6507) crested. ×20.

PLATE 16

Fig. 1.—Seeds of *N. simulans* (T.S. 315). ×20.

Fig. 2.—Seeds of *N. megalosiphon* (T.S. 271). ×20.

PLATE 17

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FURTHER NOTES ON *TRIODIA* R.BR. (GRAMINEAE) WITH DESCRIPTION OF FIVE NEW SPECIES AND ONE VARIETY

By Nancy T. Burbidge*

[*Manuscript received December* 9, 1959]

Summary

Since a revision of *Triodia* R.Br. was published some years ago (Burbidge 1953) several new species have been collected and facts concerning the distribution of others have been accumulated.

Two new species and one variety are described here from plants obtained in central Australia. Two new species from the North West Division and one from the Kimberley Division of Western Australia are also described.

The opportunity is taken to discuss the circumscription of a few species and the distribution of others formerly known only from type material.

I. Triodia pungens Group

In previous papers (Burbidge 1946*a*, 1953) a comparatively wide range of variation was accepted under the name *T. pungens* R.Br. This variation was found in the habit of the tussocks in the field and there were also differences in the spikelets, but there was no adequate basis for special treatment except at a very minor subspecific level. The variation is of little value for diagnosis in the field and of no real value in the herbarium except in the case of var. *linearis* N. T. Burbidge, separated on the basis of the small, narrow, almost glabrous spikelets, and in the Pilbara form in Western Australia, where the entire portions of the lemmas are strongly indurate and yellow in colour.

While at Kew in 1953 and 1954, the author re-examined the specimens held in the Herbarium of the Royal Botanic Gardens, and found that they included specimens of forms from central Australia which had, owing to the incomplete nature of the material studied, been somewhat dubiously included with *T. pungens*, in the Revision. Later, during a field trip to central Australia in 1955, these forms were recognized in the living state, and when examined in the herbarium the differences appeared sufficient to justify separation. As a result one form, which is always associated with the stony slopes and skeletal soils of gullies, has been described here as a new species, and another, whose distinctiveness from *T. pungens* is less satisfactory, is recognized as a variety.

Triodia hubbardii sp. nov.

Holotype.—Standley Chasm, MacDonnell Ra., central Australia, *N. T. Burbidge and M. Gray* 4153, 18.ix.1955 (CANB).

Affinis *T. pungenti* sed differens ob spiculae laxae, lemmata divaricata.

Culmi glabri. *Foliorum vaginae* striatae, resinatae. Orificia ciliata hirsuta. *Laminae* conduplicatae, resinatae; pagina inferiora media striata, lateraliter laeve.

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Panicula laxa, 30–60 cm longa; rhachi angulati, anguli scaber; spiculae racemosae, pedicellatae; pedicelli filiformes et 2–5 mm longi. *Spiculae* 5–11-floriferae, lineares, laxae, 8–14 mm longae, 3–4·5 mm latae. *Glumae* lanceolatae vel ellipticae, chartaceae, carinatae, supra medium scabra, 3–7-nervis (nervae primoris scabrae), inferior 7 mm longa, obtusa vel acuto-truncata sed mucronata; superior 5·5 mm longa, obtusa vel subtrilobata, mucronata. *Lemmata* indurata, divaricata, trilobata; lobi rigidi, erecti, subaequales vel medio longior, lobi laterales acuminati, ciliolati; lobo medio concavo, margines incurvi, ciliolati; infima lemmata 5 mm longa (callus 0·5 mm inclusis), dorso infra medium partem sparse pubescentia, item margines infra medium; callus curvatus, obliquus, lateraliter barbatus. *Paleae* ellipticae, glabrae vel supra medium scabridulae, infimae 4 mm longae, carinis alatis alae angustae ciliolatae. *Antherae* 2·75 mm longae. *Lodiculae* duae membranaceae, cuneatae.

Perennial forming large tussocks, the leaves as in *T. pungens* and highly resinous. *Laminae* to 45 cm long. *Panicles* 30–60 cm long, slender but loose, the pedicellate spikelets in lateral racemes, rhachis angular and scabrid especially on the angles. *Spikelets* loose with divaricate lemmas (which when young are partially or wholly enclosed in the purplish glumes), 5–11-flowered, linear in outline, 8–14 mm long, 3–4·5 mm wide. *Glumes* lanceolate, appearing acuminate-mucronate in side view, scabrid in the upper half, with 3 prominent scabrid nerves but usually with a pair of minor ones on either side of the mid nerve at the base; lower glume 7 mm long, apex slightly ragged or obtuse but mucronate; upper glume 5·5 mm long, shortly lobed on one side or almost trilobate. *Lemmas* indurate on the entire portion, margins incurved except for the narrow wing which extends to the lobes, a double series of short hairs along the median line in the lower half of the back and with similar hairs along the margins; callus oblique, curved, glabrous, and with a median ridge on the abaxial surface but bearded laterally, the hairs continuous with those of the lemma margins; lobes about a quarter as long as the entire portion, minutely scabridulous and ciliolate, the laterals flat and acuminate, the central one slightly longer and concave-subulate; lowest lemma 5 mm long (with the 0·5 mm callus), the 9 nerves more or less evenly spaced in the entire part. *Palea* narrow-elliptical, the lower two-thirds semi-indurate, the upper third (which lies against and is almost as long as the lobes) thin and minutely scabridulous; the nerves narrowly winged, the wings ciliolate above. *Anthers* 3, 2·75 mm long. *Lodicules* 2, thin and cuneate. (Fig. 2(*b*).)

The anatomy of the leaves places this near *T. pungens* and *T. mitchellii* Benth. From the former it differs in the narrow shortly lobed lemmas, the laterally bearded callus, the palea longer than the entire portion, and the loosely divaricate lemmas. The same features serve to distinguish it from *T. mitchellii*, with which it shares the character of a recurved palea tip, though this is not always observable. The new species differs from *T. pungens* var. *linearis* in the loose spikelets and in the vestiture of the lemmas. In immature specimens the glumes wholly enclose the lemmas, giving the spikelets an appearance quite different from that of mature ones.

The species is named in honour of Mr. C. E. Hubbard, of the Royal Botanic Gardens, Kew, whose interest in the grasses of Australia is of long standing and whose advice on the taxonomy of the Gramineae has been of the greatest assistance on many occasions.

All the specimens studied have been obtained from an area, roughly rectangular in outline, to the west and north-west of Alice Springs, with Mt. Doreen forming the north-west corner. The species is always associated with stony or rocky slopes, or with stony gullies in the ranges.

In accordance with the author's usual custom the localities are listed from west to east and from north to south.

*Specimens Examined.**—Vaughan Springs, *M. Lazarides* 6038, 18.ix.1956; also same locality, *R. E. Winkworth* 416, 4,vii.1954 (CANB); Mt. Eclipse, *J. B. Cleland*, 19.viii.1951; E. of Coniston, in creek bed, *J. B. Cleland*, 23.viii.1936 (K); Prowse's Gap near Aileron Station, *C. J. Mulhearn* 58, 27.ix.1947 (CANB); Hann's Ra., *J. B. Cleland* 354, 9.viii.1931; Mt. Liebig, in watercourse, *J. B. Cleland* L.35, 19.viii.1932 (K); Standley Chasm, MacDonnell Ra., *R. A. Perry* 5389, 4.ix.1955 (CANB).

Triodia pungens var. **parvidentata** var. nov.

Holotype.—Between Dashwood Creek and Narwietooma Station, on sandy plain, *N. T. Burbidge and M. Gray* 4314, 25.ix.1955 (CANB).

Affinis *T. pungentes* sed lobis lemmatium brevissimibus, inaequalibus.

Tussocks similar to those of others in the *T. pungens* complex but the leaves not as resinous as in *T. hubbardii* and the laminae not as long. *Panicle* narrow but loose, the spikelets racemose on short lateral branchlets bearing 4–6 spikelets. *Spikelets* shortly pedicellate, linear to lanceolate in outline, 5–9-flowered, 7–14 mm long, 3–5 mm broad, lemmas loosely imbricate but the bases not exposed as in *T. hubbardii*. *Glumes* chartaceous, the lower broadly lanceolate, 6–7 mm long, with 3 nerves of which the mid nerve is prominent, slightly scabrid above, apex narrowly obtuse and apiculate-mucronate, the margins entire or minutely ciliolate; upper glume oblong, 4·5–6 mm long, obtuse, less scabrid than the lower and separated from it by a relatively long rhachilla joint. *Lemmas* ovate or broadly lanceolate, narrowed above, shortly 3-lobed or toothed, with a well-defined series of hairs along the median line but glabrous on the margins, villous at the base where the hairs obscure the short callus; the margins thinner above and forming a wing to the lateral lobes, which are 0·75–1·25 mm long and minutely ciliolate, central lobe usually slightly longer and concave-subulate; lowest lemma 5–5·5 mm long. *Palea* elliptical, glabrous, 4·5–5 mm long, winged on the nerves, the wings minutely ciliolate above, apex fitting into the lower half of the central lobe of the lemma. (Fig. 1(*b*).)

There seems to be no satisfactory character by which this can be fully separated from *T. pungens*, though the spikelets appear quite different. The variety bears a similar relationship to *T. pungens* as *T. mitchellii* var. *breviloba* N. T. Burbidge bears to *T. mitchellii* sens. str. In *T. pungens* the lobes of the lemmas are at least a third and sometimes half as long as the entire base, which is often

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* The herbarium in which the specimens examined are housed is indicated after a citation, or after a series of citations where several specimens are in the one institution.

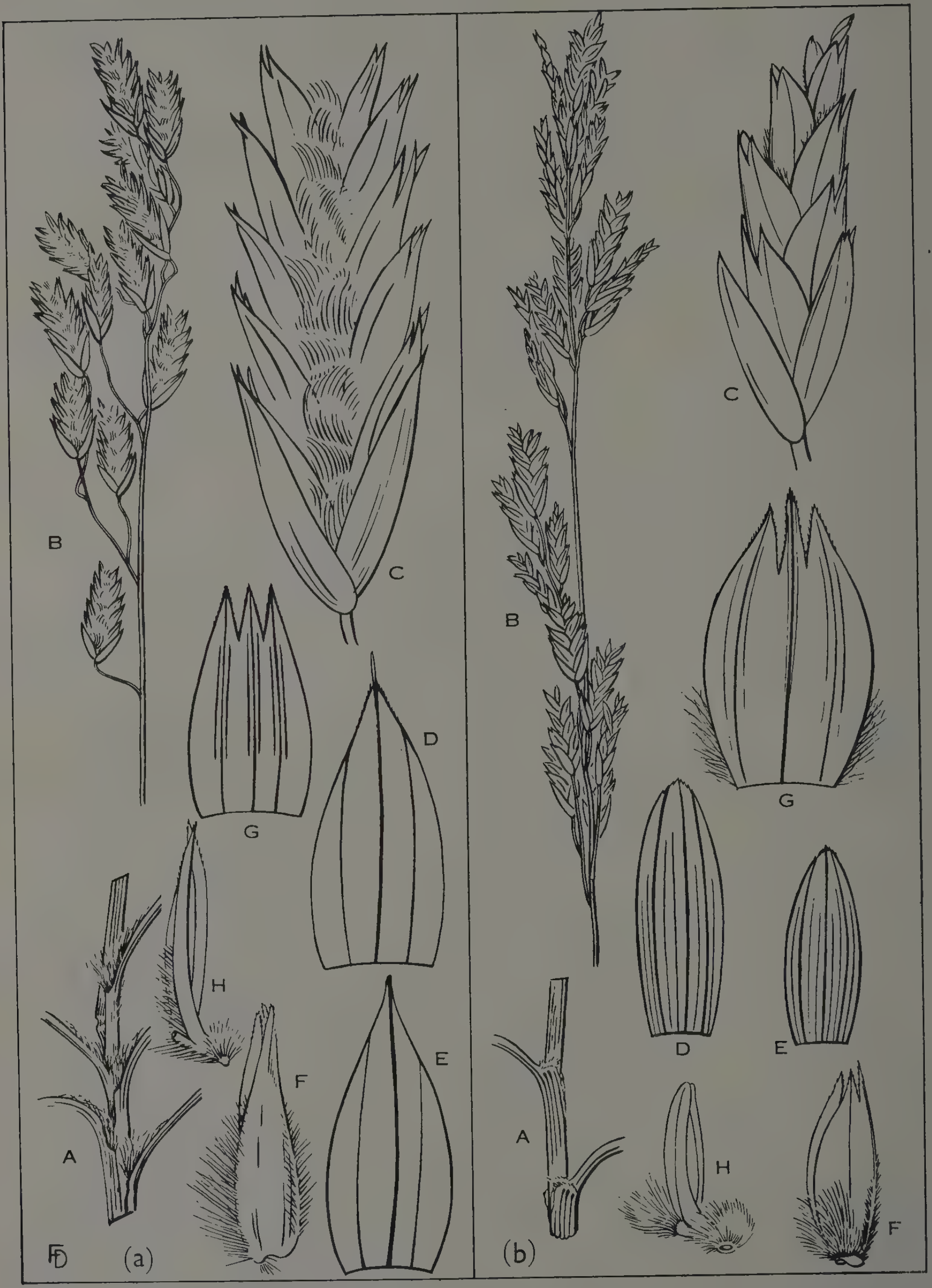

Fig. 1.—(*a*) *Triodia clelandii* sp. nov. (drawn from holotype). (*b*) *Triodia pungens* var. *parvidentata* var. nov. (from holotype). *A*, portion of culm; *B*, portion of panicle; *C*, spikelet; *D*, lower glume; *E*, upper glume; *F*, lemma in side view; *G*, lemma from within; *H*, palea.

stiffly indurate and yellowish in colour. The palea is usually slightly shorter than or as long as the entire portion, though in some Queensland material it may be long enough to fit into the groove of the median lobe of the lemma. In the new variety the hairs of the base of the lemma are not extended along the margins. In *T. pungens* sens. str., though always present, they vary in their development. In *T. pungens* var. *linearis* the hairs of the lemma are limited to a very short basal series.

When dissecting spikelets it is usual to find that a portion, at least, of the next rhachilla joint remains attached to the curve of the base of the palea. In most cases this rhachilla joint is glabrous or possibly scabrid, but in some it has a dense tuft of hairs at the top. This tuft, which has been observed in other species also, appears to represent part of the hairs of the callus of the succeeding floret, but the manner of the fracture of the callus is not properly understood.

The variety is found in the spinifex communities of the plains adjacent to the ranges in central Australia.

Specimens Examined.—18 miles NNW. of Narwietooma, *R. E. Winkworth* 347, 10.vi.1954; 4 miles SW. of No. 2 Desert Bore, Hamilton Downs, *G. Chippendale* 1739, 23.ix.1955 (CANB); N. Petermann Ranges, *H. Basedow* Nos. 184, 185, July 1926; sandhills between Ayers Rock and Musgrave Ranges, *H. Basedow* 79, June 1926; N. of Kelly Hills (N. of Musgrave Ra.), *H. Basedow* 74, June 1926 (K).

A certain amount of variation is found between these specimens. In the holotype and in *Basedow* 74 and 185 the glumes are relatively short and the lemmas exposed, in *Basedow* 79 and 184 and in *Chippendale* 1739 the glumes are relatively long and, particularly in the immature Basedow material, enclose the rest of the spikelet to a greater degree. *Winkworth* 347 is intermediate in this character. The Kew sheet of *Basedow* 79 bears a note by J. M. Black stating that he thought it a variety of *T. irritans* R.Br. The presence of resin and the typical *pungens* leaf form, quite apart from the spikelet characters, make this placing quite incorrect.

II. FOUR NEW SPECIES

Among the material seen at Kew was an undescribed species the specimens of which had been placed together by Mr. C. E. Hubbard, who proposed to name it after its collector, Professor J. B. Cleland of Adelaide, whose collections and active interest have contributed much to our knowledge of Australian plants. With Mr. Hubbard's kind permission this species is described below, the type being a more recently collected specimen.

A further two species have been discovered as a result of collecting by Dr. N. Speck, of the Land Research and Regional Survey Division, C.S.I.R.O., while engaged on a survey of the country in the vicinity of Wiluna in central Western Australia. These, with another collected by Lazarides in the Kimberley Division, are described below.

Triodia clelandii sp. nov.

Holotype.—Vicinity of Haast's Bluff, central Australia, on rocky scree of isolated hill, *N. T. Burbidge and M. Gray* 4286, 24.ix.1955 (CANB).

Affinis *T. brizoides* et *T. burkensis* sed paniculis nutantibus, spiculis longioribus, 7–15-floriferis.

Culmi et nodi glabri. *Foliorum vaginae* hirsutae vel glabrescentes. Orificia hirsuta; pili flaccidi laxe implicati. *Laminae* rigidae, glabrae, pungentes. *Panicula* exserta, laxa, nutans, 10–15 cm longa. *Spiculae* pedicellatae, ovatae vel oblongo-lineares, lateraliter compressae, 12–22 mm longae, 7–15-floriferae; pedicelli scabriduli, ad 12 mm longi. *Glumae* subaequales, lanceolatae, acuminatae, mucronatae, glabrae vel minute scabridulae, 3-nervis, chartaceae, 7–9 mm longae. *Lemmata* lanceolata vel ovata, trilobata, chartaceae, carinis infra medium et marginibus ad basim dense villosis, infima lemmata 7–10 mm longa (lobis inclusis); lobi triangulares vel lineari-triangulares, acuti vel acuminati, ciliati, 0·75–3 mm longi, lobo medium concavo. *Paleae* ellipticae vel anguste lanceolatae, infra medium villosis vel glabris; carinis alatis, alis angustissimis sed ad apicibus ciliatis; apice membranaceae, angustissimae, ciliatae, in cavis medio lobo lemmatibus inclusis. *Antherae* 3–4 mm longae. *Lodiculae* duae, cuneatae.

Perennial tussocks, leaf blades dark green when fresh. *Sheaths* glabrescent but clothed with flaccid appressed hairs below the orifices on young vigorously growing shoots. Orifices with flaccid hairs to 4 mm long, the hairs commonly slightly crimped or tangled and continued on to the petiole-like bases of the laminae, which are otherwise glabrous. *Laminae* conduplicate-terete, smooth but obscurely striate under a lens, the apices slender and pungent-pointed. *Panicles* much exserted from the uppermost sheaths, drooping or nodding to one side, 10–15 cm long, the spikelets pedicellate on filiform pedicels which, like the rhachis, are minutely scabrid. *Spikelets* ovate to linear-oblong, much flattened laterally, 12–22 mm long (dependent on the number of florets), 7–15-flowered. *Glumes* subequal, lanceolate, acuminate-mucronate, 3-nerved or sometimes with 1 or 2 short additional nerves at the base, the mid nerve prominent in the upper half, chartaceous, 7–9 mm long. *Lemmas* broadly lanceolate or ovate, densely bearded on the short callus, with a series of dense hairs up the median line of the back and with longer hairs developed submarginally in the lower third; the 3 lobes less than a quarter as long as the entire part, the lateral lobes usually slightly shorter than the central lobe, triangular in outline with acute or acuminate-subulate apices ciliate on the margins, the central lobe linear or almost subulate but the margins incurved and ciliolate with sparse minute hairs on the inner face; the lowest 1 or 2 lemmas 7–10 mm long. *Palea* elliptical or lanceolate, narrowly winged on the nerves, the wings ciliolate above the middle, the apex with a very narrow membranous prolongation which, in a folded position, fits into the groove of the central lobe of the lemma. In some specimens the palea is glabrous, in others there are long hairs in the basal quarter or low on the nerves, in which case the wings may be ciliate rather than ciliolate above. *Anthers* 3–4 mm long. *Lodicules* 2, cuneate. (Fig. 1(*a*).)

The species is widespread on stony ground and on the slopes of low, often isolated ranges in central Australia.

Specimens Examined.—25 miles SW. of Napperby, N.T., *M. Lazarides* 6002, 16.ix.1956 (CANB); Mt. Liebig, *J. B. Cleland* L.28, 14.viii.1932 (also L.29, 19.viii.1932; L.30, 14.viii.1932; L.37, 11.viii.1932; L.40, 13.viii.1932); amongst stones near watercourse, Mt. Liebig, *J. B. Cleland*

L.31, 13.viii.1932; top of Mt. Liebig, *J. B. Cleland* L.32, L.33, 14.viii.1932; Haast's Bluff, *J. B. Cleland* L.39, 8.vii.1932 (K); Haast's Bluff, *R. E. Winkworth* 673, 9.x.1954; Haast's Bluff area, *G. Chippendale* 2559, 23.viii.1956; 10 miles NE. of Haast's Bluff Mission Station, *N. Forde* 840, 25.vi.1957; between Gosse's Bluff and MacDonnell Ra., on gibber rise, *N. T. Burbidge and M. Gray* 4273, 23.ix.1955; 2 miles S. of Hermannsburg Mission, on river bank, *R. A. Perry* 5393, 5.ix.1955; Standley Chasm, *R. A. Perry* 5388, 4.ix.1955; Standley Chasm, MacDonnell Ra., on rocky slopes, *N. T. Burbidge and M. Gray* 4152, 18.ix.1955 (CANB).

This species has been confused with *T. brizoides* N. T. Burbidge, *T. wiseana* C. A. Gardner (under which *Cleland* L.32 was quoted in the Revision), and *T. burkensis* N. T. Burbidge, which does not occur so far south. From *T. brizoides* it differs in the longer and non-glaucous leaves, the flaccid not woolly hairs of the leaf orifices, the dark green leaves, and the drooping panicles. The comparison with *T. wiseana* is partly based on the similarity of the orifice hairs. In *T. clelandii* these are crumpled and not spreading and, furthermore, they do not arise in tufts. The spikelets are different, but this character is less readily seen in immature specimens. In *T. burkensis* the leaves are pale when fresh and the spikelets are smaller. These differences are tabulated in Table 1.

As constituted, *T. clelandii* includes a certain amount of variation in the length of the lemma lobes, the number of florets per spikelet, the density of the hairs on the lemmas, and the presence or absence of hairs at the base of the palea. There is some evidence that the species is developing local variants on the isolated hills and other sites from which it has been collected. Thus *Perry* 5393 and *Burbidge and Gray* 4273 have glabrous paleas. The remaining specimens have hairy paleas, but some are densely hairy at the base while in others the hairs are few and limited to the nerves. The lemmas of the Haast's Bluff specimens have longer lobes than those of the Standley Chasm plants, and those of the Mt. Liebig specimens are longer still and more subulate.

In young panicles the submarginal hairs of the lemmas may be obscured, a feature which increases the resemblance to *T. wiseana*, while in older spikelets or in those with very dense and copious hairs there may appear to be a median beard along the flat sides of the spikelets. In this case there is a stronger resemblance to *T. brizoides* in herbarium specimens.

Triodia concinna sp. nov.

Holotype.—S. of Meekatharra–Wiluna railway, 30 miles W. of Wiluna, W.A., *N. Speck* 1482, Sept. 1958 (CANB).

Affinis *T. inutile* sed spiculae purpurascentes, late ovatae, lemmata tridentata non trilobata.

Culmi glabri. *Foliorum vaginae* striatae, margines ciliatae. Orificia tomentosa, tomentum villosum implicatum. *Laminae* rigidae, brevae, 3–7 cm longae, striatae, glabrae, pungentes. *Panicula* oblonga, 4–8 cm longa, rhachis et rami glabri. *Spiculae* compressae vel turgidae, late ovatae vel ovatae, purpurascentes, 5–7-floriferae, pedicellatae, 8–12 mm longae, 5–6 mm latae. *Glumae* ovato-lanceolatae, obtusae, apiculatae, subaequales, 4·5–5 mm longae, 5-nervis, nervae prominentes, ad apicis ciliolatibus. *Lemmata* ovata, naviculata, tridentata, dentae incurvae, ad basim villosa, infima lemmata 5 mm longa, callus glabrus. *Paleae* ellipticae vel late lanceolatae, glabrae vel ad basim villosae, carinis alatis, alis latissimis, marginis ciliolatibus, infima 4·5 mm longa. *Antherae* 2·5 mm longae. *Lodiculae* duae, cuneatae.

TABLE 1

COMPARATIVE FEATURES OF T. CLELANDII AND SIMILAR SPECIES

T. clelandii	*T. brizoides*	*T. wiseana*	*T. burkensis*
Leaf blades dark vivid green when fresh	Leaf blades glaucous	Leaf blades dull green when fresh	Leaf blades pale green
Orifice hairs flaccid, crumpled or tangled	Orifice hairs woolly and tangled	Orifice hairs flaccid but spreading, not tangled	Orifice hairs flaccid but tangled
Panicles drooping	Panicles erect with spreading branches	Panicles erect with spreading branches	Panicles erect with spreading branches
Spikelets ovate to oblong, 12–22 mm long, 7–15-flowered	Spikelets oblong, 10–20 mm long, 6–8 mm wide, 7–10-flowered	Spikelets oblong to linear-lanceolate, 8–12 mm long, 5–9-flowered	Spikelets ovate or oblong, 6–11 mm long, 4–7-flowered
Glumes 3-nerved, 7–9 mm long, lanceolate, acuminate	Glumes oblong, 3–5-nerved, 6–6·5 mm long	Glumes oblong to lanceolate, 3–5-nerved, 4·5–5 mm long	Glumes broadly lanceolate to oblong-lanceolate, 3–5-nerved, 4–5·5 mm long
Lowest lemma 7–10 mm long, lateral lobes acute-acuminate, central lobe linear-concave	Lowest lemma 5–7 mm long, lobes narrowly acute-acuminate, central one narrow concave	Lowest lemma 4–6 mm long, lobes acuminate, central one narrower and concave	Lowest lemma 5·5–6 mm long. Lobes as in *T. clelandii*
Submarginal hairs of lemma on lower third to half	Submarginal hairs extending to base of lobes	Submarginal hairs near base only	Submarginal hairs extending two-thirds length of entire portion
Paleal nerves very narrowly winged. Apex with a folded prolongation fitting into the groove of central lobe of lemma	Paleal nerves very narrowly winged. Prolongation sometimes present	Paleal nerves winged, the wings often visible outside the margins of the lemma. No prolongation	Paleal nerves narrowly winged sometimes protrudent. No prolongation

Forming dense tussocks, the culms glabrous but the leaf sheaths ciliate on the upper margins and with tangled woolly hairs at the orifices, with short petiole-like bases to the short laminae. Panicles exserted and standing well up from the

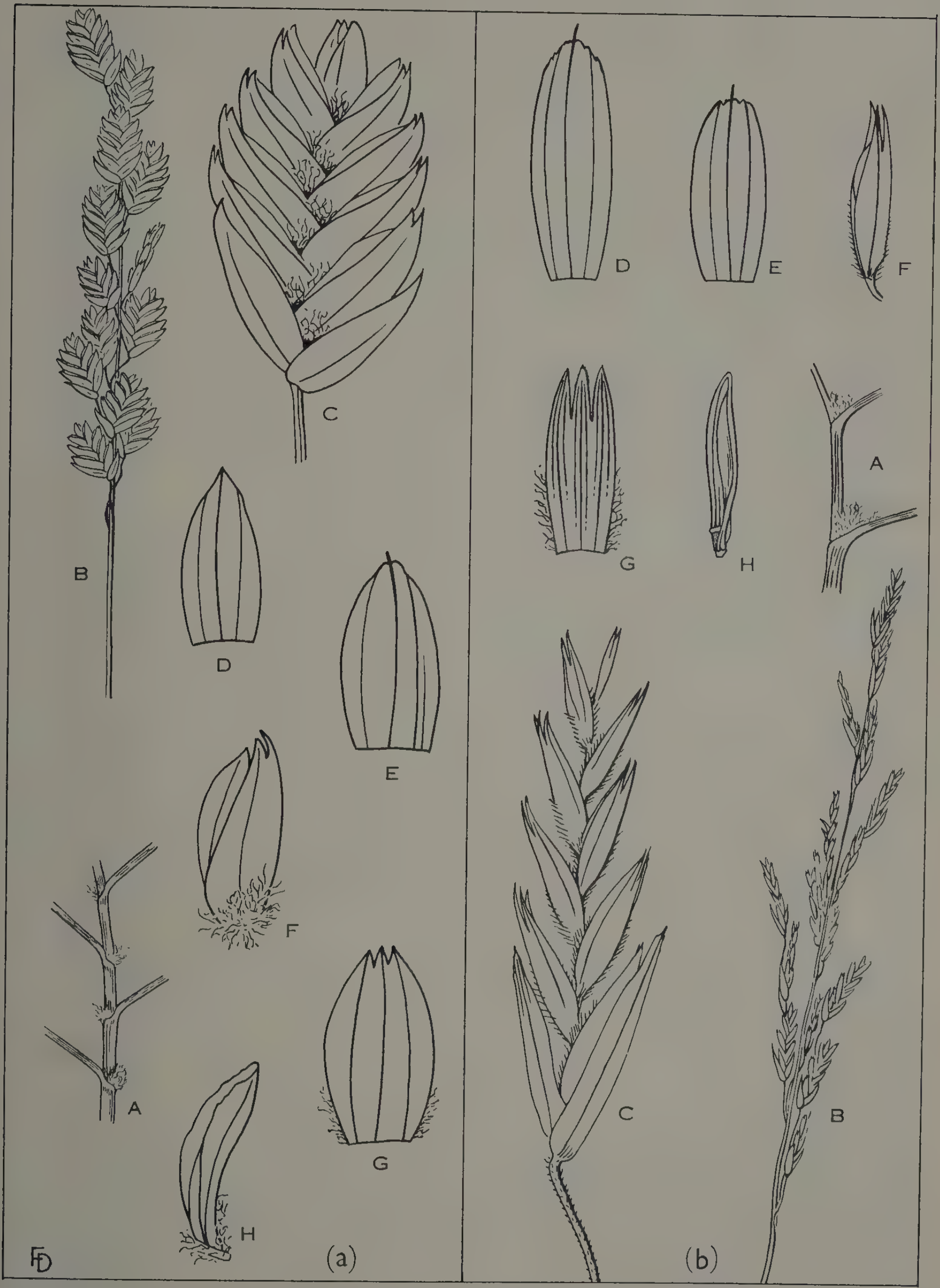
B
C
D
E
F
A
G
H
FD
(a)
D
E
F
G
H
A
C
B
(b)

Fig. 2.—(*a*) *Triodia concinna* sp. nov. (from holotype). (*b*) *Triodia hubbardii* sp. nov. (from holotype). *A–H*, as in Fig. 1.

short leafy shoots, pedicels and rhachis glabrous. *Spikelets* dark purplish (pale when old), the lower ones in pairs, much compressed from the sides but becoming plump when older, broadly ovate in outline. *Glumes* broadly lanceolate or ovate and naviculate, with prominent nerves of which 3 reach the apex, 4·5–5 mm long, subequal but the upper glume usually slightly longer and sometimes subtridentate. *Lemmas* broadly ovate and naviculate, shortly tridentate with the teeth incurved, glabrous apart from the soft hairs arising from the lower third, the short oblique callus glabrous. *Palea* elliptical or lanceolate apart from the projecting wings (about 0·5 mm wide), the narrow apex and the margin of the paleal wings minutely ciliolate, the adaxial surface glabrous or with villose hairs at the base. *Anthers* pale, 2·5 mm long. *Lodicules* 2, cuneate and thin. (Fig. 2(*a*).)

In the holotype the spikelets are much flattened and dark purple in colour. The paleas are glabrous. In a further specimen, *N. Speck* 1480, "2½ miles S. of railway line, 32 miles W. of Wiluna, Eremaean Province, Western Australia, 18.ix.1958", the panicles are overmature. In this the spikelets are plump, and it is possibly due to this that they appear narrower than the spikelets of the holotype. The paleas have a tuft of soft woolly hairs at the base.

In a third specimen, *Speck* 1450, "Sandstone Road, 17 miles S. of Wiluna, Western Australia, 12.ix.1958" only leafy culms are available. It is placed with *T. concinna* because it has a similar type of leaf anatomy. Superficially it resembles a sparsely woolly form of *T. basedowii* Pritzel, but when sectioned the laminae prove to have only one pair of subsidiary nerves on either side of the mid nerve, not the two which are characteristic of *T. basedowii* (Burbidge 1946*c*).

Apart from the vegetative resemblance to *T. basedowii* this species is very distinct. The broadly winged paleas are not so conspicuous as in *T. intermedia* Cheel. In the key published in 1953 it appears to lie near *T. inutilis* N. T. Burbidge, but differs in the size, colour, and shape of the spikelets and the very shortly lobed lemmas. So far as is known, *T. concinna* is restricted to the area between Meekatharra, Wiluna, and Sandstone in central Western Australia.

Triodia plurinervata sp. nov.

Holotype.—Dorre I., Shark Bay, W.A., *R. D. Royce* 5884, 15.vii.1959. "Clumps 1–2 feet high, up to 8 feet diameter, in rings or clumps, red sandy soil".

Affinis *T. spicatae* sed ligulis brevioribus, spiculis pedicellatis, lemmatis tridentatis plurinervatis.

Culmi glabri. *Foliorum vaginae* glabrae, orificia ciliolata, ligulae ciliolatae. *Laminae* graciles rigidae glabrae pungentes. *Panicula* subspicata angusta, 6–10 cm longa. *Spiculae* linearea vel angustes lanceolatae, 12–15 mm longae, 6–8-floriferae, pedicelli brevissimi. *Glumae* lanceolatae subaequales, 4–5 mm longae, acutae vel obtusae, 5–9-nervis, nervae prominentes. *Lemmata* ovata vel oblongo-lanceolata indurata, 11–13-nervis, dorso infra mediam partem villosa supra mediam striata, tridentata, infima ad 6 mm longa. *Paleae* incurvae glabrae vel ad basim villosae, carinis angustis ciliolatis. *Antherae* 3 mm longae purpurascentes. *Lodiculae* duae cuneatae induratae recurvae apiculatae. (Fig. 3(*b*).)

Culms and *leaf sheaths* glabrous, the orifices and ligules shortly ciliolate, the *laminae* slender, glabrous, and pungent-pointed. *Panicle* a simple subspicate raceme with alternately arranged very shortly pedicellate spikelets. *Spikelets* linear to lanceolate, 12–15 mm long, 6–8-flowered. *Glumes* lanceolate, subequal or the upper slightly longer, 4–5 mm long with the apex acute or obtuse but sometimes appearing acuminate due to the incurved margins, 5–9-nerved with the nerves prominent but usually asymmetrically arranged. *Lemmas* 11–13-nerved, ovate or oblong-lanceolate and shortly tridentate, the lobes rigid incurved ciliolate and subequal, the back of the lemma villous below with soft hairs which are also on the short callus and may be continued higher near the margins, the upper portion striate but glabrous or scabridulous towards the ciliolate margins. *Palea* slightly shorter than its lemma especially in the lower florets, incurved over the floral organs, glabrous on the back in the type, the nerves rigid towards the base but narrowly winged above, the wings minutely ciliolate.

This species is distinguished from all others known by its simple racemose panicle and by the unusually numerous nerves of the lemmas. In other species the lemma has three sets of three nerves, each set being associated with the tissue below or in a lobe. In *T. plurinervata* there is an additional nerve between the margin and the lateral triads and another between the lateral triads and the central one (making four additional nerves). The species has the short ligular and orifice hairs of members of the *T. irritans* group, but the simple panicle resembles the spicate type found in *T. spicata* N. T. Burbidge, which differs in lacking the tridentate lemmas and in the sessile spikelets.

The distinctiveness of this species was first recognized in a specimen, *N. Speck* 1434, "18 miles W. of Yelma (abandoned station), 99 miles E. of Wiluna, W.A., 11.ix.1958" (CANB). Unfortunately the material is not only overmature but the spikelets are malformed owing to infestation by the larvae of a chalcid wasp. The result of this, judging from the Dorre Island specimen, has been to produce longer and very turgid spikelets in which the paleas, which are villose on the back, are commonly only half as long as their lemmas and may have the inner folds enlarged to overlap about the remains of the floral organs. The general aspect is somewhat different from that in the Dorre Island plant, as the panicle is more elongated, but it is believed that the differences are due to the malformation. Presence or absence of hairs on the palea has not proved a sound diagnostic character in other species, though it is possible that some morphological differentiation at the subspecific level may be present between the mainland and island populations of the species.

Triodia inaequiloba sp. nov.

Holotype.—One mile E. of Mt. Amherst Homestead, Kimberley Division, W.A., *M. Lazarides* 6343, 15.vii.1959 (CANB).

Affinis *T. wiseana* sed lemmata cum lobis uninervibus inaequalibus et carinatis differt.

Foliorum vaginae sparse lanatae. Orificia tomentosa, tomentum flaccida. *Laminae* rigidae striatae glabrae pungentes. *Panicula* 10–15 cm longa. *Spiculae* ovatae 4–6-floriferae, 7–9 mm longae, 4–5 mm latae, pedicellatae pedicelli brevi.

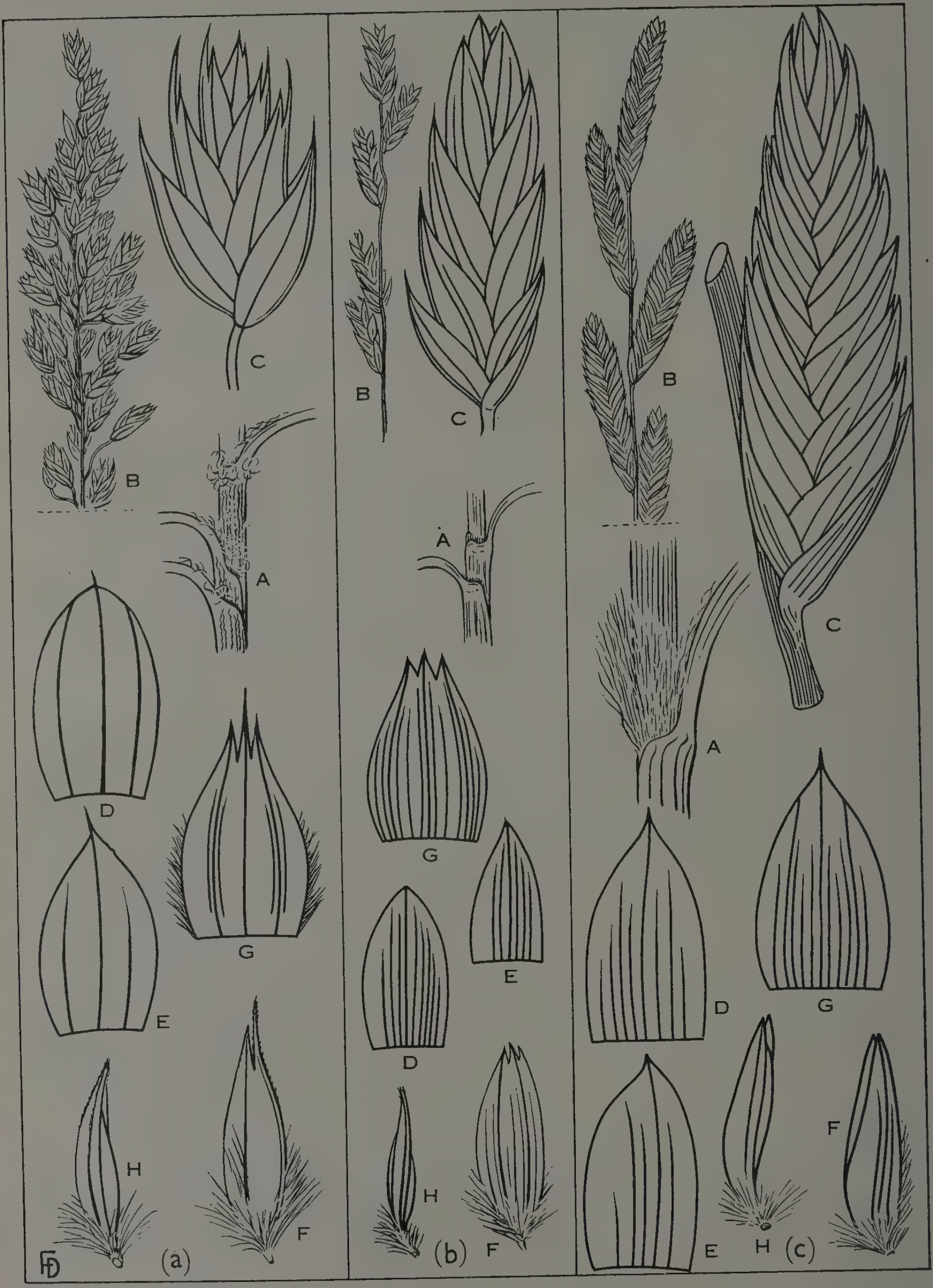
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Fig. 3.—(*a*) *Triodia inaequiloba* sp. nov. (from holotype). (*b*) *Triodia plurinervata* sp. nov. (from holotype). (*c*) *Triodia spicata* N. T. Burbidge (from *Lazarides* 5780). *A–H*, as in Fig. 1.

Glumae ovatae aequales chartaceae 3-nervis, medio nervo prominente mucronatae, 5–6 mm longae scabridulae. *Lemmata* ovata chartacea, dorso infra mediam partem villosa, item margines prope basim, trilobata, lobi carinati uninervati scabriduli ciliolati, apices subulati, lobo medio longioris; infima lemmata 6–6·5 mm longa, callus minutus, breve villosus. *Paleae* membranaceae, supra medium scabridulae, ellipticae, infimae 5–5·5 mm longae, nervis alatis, alae angustae ciliolatae, nervae rigidae.

Forming large tussocks to more than 1 m in diameter and almost as high. Foliage bright green when fresh. *Leaf sheaths* sparsely woolly or glabrescent, orifice with flaccid woolly hairs up to 5 mm long developed from the top of the sheath and from the adaxial face of the petiole-like base of the lamina, the true ligule short and ciliate; laminae slender, minutely striate, pungent-pointed. *Panicle* lanceolate or ovate in outline, the spikelets shortly pedicellate along short branches which have a small tuft of hairs in their axils on the main rhachis. *Spikelets* ovate or broadly lanceolate, rather loose or at least not turgidly imbricate, 4–6-flowered, 7–9 mm long and more than half as wide at the broadest point. *Glumes* naviculate but ovate, equal, chartaceous or stiffly scarious in texture, minutely scabridulous, the prominent mid nerve produced as a mucro, the lower glume with a pair of obscure lateral nerves, the upper with a pair of prominent lateral nerves. *Lemmas* ovate, chartaceous, with a tuft of hairs on the back below the middle and with similar hairs towards the base and near the margins on either side, above the middle glabrous or minutely scabridulous especially on the lobes, with 3 groups of 3 nerves in the lower part of the entire portion, one of each triad becoming prominent and continued one into each lobe; the lobes markedly unequal with the median one (unless broken) about twice as long as the laterals, lobes subulate at the apices and minutely ciliolate; the callus short, blunt, and shortly villose. *Palea* elliptical, glabrous or scabridulous in the upper third, the nerves rigid and narrowly winged, ciliolate towards the narrow apex which fits into the median lobe of the lemma, slightly shorter than its lemma (Fig. 3(*a*)).

This species might superficially suggest *T. wiseana* C. A. Gardner but it differs in the woolly, almost scurfy, hairs at the orifices of the leaf sheaths and in the unequal lobes of the lemmas. The lobes are, furthermore, distinctly ridged by the single nerve in each. The species is only known from the holotype material, which was obtained in the south-east of the Kimberley Division and to the west of Hall's Creek.

III. Notes on Various Species

Note A

Under *T. procera* R.Br. in the "Flora Australiensis" Bentham (1878) listed a specimen "Victoria River, Mueller". The sheet representing this at Kew bears a specimen of *T. pungens* var. *linearis* N. T. Burbidge. It has the panicle of *T. pungens*, the glumes are somewhat longer than in the type of the variety (both actually and in proportion to the spikelets), but the specimen matches *Perry* 1889 quoted with the original description of the variety.

Note B

T. brizoides N. T. Burbidge was recently collected in a locality on Mulga Downs, N. of the Hammersley Ra. in Western Australia. This is to the south and west of previously recorded sites. The specimen is *Burbidge* 5994, obtained on 6.v.1958. It was growing on a barren stony slope of an ironstone ridge of the breakaway type, forming a community with very few associated ephemerals.

Notes on other species in the Hammersley Ra. area and the Pilbara district of Western Australia have been provided in a recent paper (Burbidge 1959).

Note C

T. plectrachnoides N. T. Burbidge has been re-collected at Dillon Springs, 46 miles SE. of Wyndham township, W.A., *M. Lazarides* 3168, 10.viii.1952 (CANB). The material differs from the original in having the lower lemmas nearly twice as long as the glumes. This increases the resemblance to a *Plectrachne*, but the ellipsoidal outline of the spikelet, though narrow, is more that of a *Triodia*.

In the key, given in the Revision (Burbidge 1953), this species was placed with those whose laminae are not thickened in the median third but which are evenly striate on the lower surface. In the original description the leaves are stated to be smooth and glabrous except at the orifices. Closer study of *Lazarides* 3168 shows that this is correct, but when sectioned the blades proved to have an internal anatomy which closely resembles that of *Plectrachne schinzii* Henr. as figured by the author (Burbidge 1946*b*, Plate 3, Fig. 1). That is to say, it has the "pungens" type of leaf anatomy. Lazarides describes the leaves as non-resinous, but in his specimen there are traces of dried resin at the orifices. Since the species is slightly resinous it is possible that attempts will be made to place it among species related to *T. pungens*, by persons using the key in the Revision. It may be distinguished from all of these by the remarkably long pedicels and by the slender subulate awn-like lobes of the lemmas.

Unfortunately the fragment of the type, held at Canberra, consists of two overmature panicles, and a search has failed to locate the remainder of the material at Brisbane. Consequently it has not been possible to check this matter with the type.

Note D

T. spicata N. T. Burbidge has now been collected from other localities in the Northern Territory, as follows:

25 miles S. of Hooker Creek, *R. A. Perry* 2915, 21.vi.1952; 10 miles SW. of Barrow Creek, *R. E. Winkworth* 883, 9.iii.1955; hill near Yuendumu, *J. B. Cleland*, 24.viii.1951; 2 miles S. of Aileron, *R. E. Winkworth* 923, 20.iii.1955; 12 miles SE. of Aileron, *M. Lazarides* 5780, 22.viii.1956. (See Fig. 3(*c*).)

All these specimens are held in the Herbarium of the Division of Plant Industry in Canberra.

IV. ACKNOWLEDGMENTS

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